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# "On" and "off" channels in the human visual system

by

© Lew B. Stelmach

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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IN

PSYCHOLOGY

DEPARTMENT OF PSYCHOLOGY

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Abstract

Three experiments were conducted to evaluate the hypothesis that "on" and "off" responses may be processed by separate channels in the visual system. A method often used to demonstrate the independence of channels was adopted in the present research. The method measures an observer's ability to detect the presence of a signal when the noise level in the hypothesized channel transmitting the signal is either high or low. If the signal is accurately detected by the observer when the task-relevant channel is noise-free and other channels have a high level of noise, and if the signal is difficult to detect when the task-relevant channel has a high noise level and other channels are noise-free, a channel interpretation is consistent with the data.

The observers viewed a display containing small luminous elements, the contextual elements, and their task was to detect the onset or offset of one element, the focal element. It was assumed that the onset of an element produced a neural "on" response and the offset of an element a neural "off" response. The neural response to the focal element was considered to be the signal and the neural responses to the contextual elements were considered to be noise. "On" and "off" responses to the contextual elements were produced by introducing an inter-stimulus interval (Experiment 1) or a sudden shift in luminance (Experiments 2 and 3). It was assumed that an upwards shift in luminance would produce "on" responses and a downwards shift would

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produce "off" responses. The amount of noise was varied by manipulating the number of contextual elements (Experiments 1 and 2) and the magnitude of the sudden shift in lumiance (Experiment 3).

The focal element was easy to detect when it produced an "on" response in the context of "off" resposnes or when it produced an "off" response in the context of "on" responses. The focal element was difficult to detect when it produced an "on" response in the context of "on" responses and when it produced an "off" response in the context of "off" responses. The results suggest that the signal (the neural response to the focal element) was difficult to detect when the signal and noise (the neural responses to the contextual elements) were the same (both "on" or both "off") and was easy to detect when the signal and noise were different (one "on" the other "off"). Furthermore increasing noise by increasing the number of contextual elements or by increasing the magnitude of the shift in luminance caused performance to decrease primarily when the signal and noise were the same and was ineffective when the signal and noise differed. In general the results were consistent with the hypothesis that "on" and "off" responses may be processed by separate channels.

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I would like to thank V. Di Lollo, C. Bourassa, A. Friedman, A. Dobbs, A. French, and M. Horn for their assistance throughout this research and during the manuscript preparation. I am also grateful to G. Lechelt, D. Curtis, and R. Bouffard for helpful comments about particular issues in the research.

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# I. Introduction

The discovery of "on" and "off" cells in the visual system by Hartline (1938) and of a center-surround organization of receptive fields of retinal cells by Kuffler(1953) inspired a large amount of research about "on" and "off" cells and their receptive field organization. "On" cells respond to increments in luminance, whereas "off" cells respond to decrements in luminance. This is true only if the stimulus is presented to the receptive field center of the cell. The same stimulus will inhibit the cell if presented to the surround. This early research was primarily physiological and was directed at describing various properties of the cells: the shapes of the receptive fields (Hubel and Wiesel, 1961), sensitivity distributions within receptive field centers (Creutzfeldt, Sakman, Scheich and Korn, 1970), the inhibitory mechanisms of the center and surround (Maffei and Fiorentini, 1972; Poggio, Baker, Lamarre and Sanseverino, 1969; Singer, Poppel, Creutzfeldt,1972), and the intensity response functions of the cells (De Valois, Jacobs, and Jones, 1962). For reviews see Bishop (1967) and Freund (1973).

The theoretical significance of "on" and "off" cells was discussed by Hubel and Wiesel (1962), who proposed a hierarchical model of the organization of receptive fields in the visual system. They suggested that receptive fields at each stage of the visual system were constructed from receptive fields of the previous stages. In their model



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receptive fields of "on" and "off" cells in lateral geniculate nucleus organized the input to the receptive fields of cells in the cortex.

A minimal amount of psychophysical work has been concerned with "on" and "off" cells and their responses ("on" and "off" responses), and none of it is recent. Using the increment threshold method, Westheimer (1967) was able to demonstrate a center-surround organization of receptive fields in the human visual system. The increment threshold method requires the observer to detect a small test spot superimposed upon a larger conditioning field. Westheimer (1967) measured the threshold of a 1′ test spot on a variable size conditioning field (5′-20′). He found that the threshold of the test spot increased and then decreased as the size of the conditioning field increased.

Bartley and Nelson (1960) investigated the role of "on" and "off" responses in producing critical flicker frequency. The critical flicker frequency was higher when an intermittent stimulus produced "off" responses. They suggested that variations in critical frequency may depend in part on the presence and strength of "off" responses in the visual system.

Phillips and Singer (1974) and Singer and Phillips (1974) suggested that "on" and "off" cells may play a more complex and significant role in early visual processing. They suggested that inhibitory interactions between "on" and "off" cells may attenuate neural responses to objects which

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remain constant in a visual scene but transmit with full intensity responses to objects which change in a visual scene. Thus, objects which appear or dissappear from a visual scene are expected to produce stronger responses in the visual system than objects which remain constant. A psychophysical study of "on" and "off" responses was conducted by Phillips and Singer (1974) and a neurophysiological study was conducted by Singer and Phillips (1974).

The work of Phillips and Singer

In their psychophysical work, Phillips and Singer(1974) investigated human observers' ability to detect changes in visual displays. These changes were either appearances or disappearances of individual elements from a set of like elements. The elements were luminous squares subtending a visual angle of 10′ and were organized into a 10 x 10 matrix subtending a visual angle of 3°10′. The luminance of the elements was also constant, and the minimum separation between them was 10′. On any given trial a random set of elements (50 on average) appeared for some duration (T1) then, following a blank interval (ISI), the set reappeared for some duration (T2). The observer judged whether the second set differed from the first. He or she was not required to indicate the type of change, only whether a change had occurred. On 25% of the trials there was an addition of one element in T2, on 25% of the trials there was a subtraction in T2, and on 50% of the trials there was

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no change. The durations of T1, ISI, and T2 were blocked, so that within a set of trials they did not vary. The results obtained by Phillips and Singer(1974) in an experiment, where the duration of T1 an T2 were constant at 500 msec and the duration of the ISI was varied are presented in Figure 1. Performance dropped as the ISI increased and additions were detected with greater accuracy than subtractions. These psychophysical results were consistent with a physiological theory of neural functioning of the lateral geniculate nucleus (LGN) proposed by Phillips and Singer(1974). The theory describes how inhibitory interactions between "on" and "off" cells in the LGN could provide a basis for detecting the addition or subtraction. In particular it assumes that, as an element appears, it produces an "on" response in the "on" cells, and as it dissappears it produces an "off" response in the "off" cells. "On" and "off" cells inhibit each other (antagonistic or reciprocal inhibition). In the experimental display each element initially appears at the onset of T1, dissappears at the offset of T1 and reappears at the onset of T2. All elements finally dissappear at the offset of T2. It is assumed that each onset produces an "on" response and each offset an "off" response. However, due to the inhibitory interactions of the "on" and "off" cells, all "on" responses and all "off" responses are not identical.

These relationships are represented schematically in Figure 2. According to the theory, at short ISIs, the "on"

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Figure 1. Percent correct responses plotted as a function of the inter-stimulus interval between T1 and T2. Adapted from Phillips and Singer (1974).

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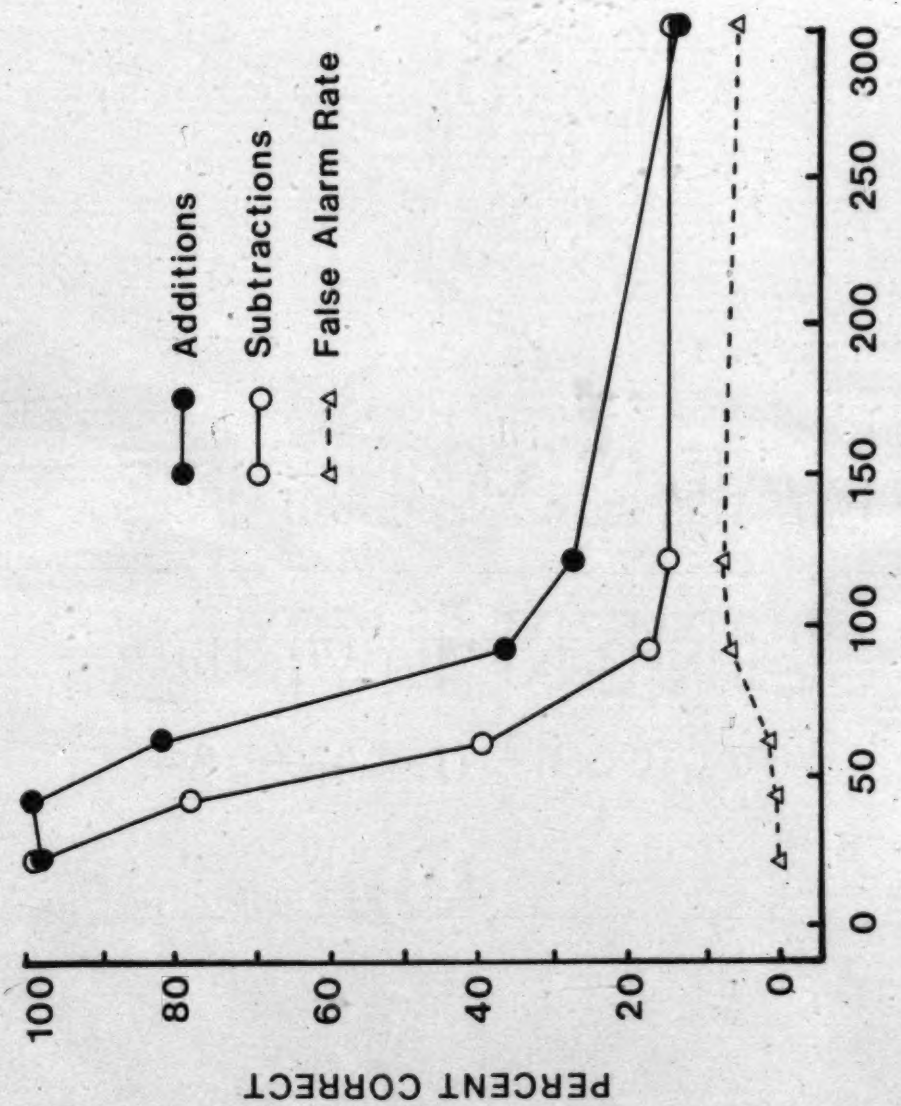
Additions
Subtractions
False Alarm Rate
PERCENT CORRECT
100
80
60
40
20
0
0
50
100
150
200
250
300
ISI (MSEC)

Figure 2. The temporal parameters in Experiment 1 are shown at the top of the figure. Hypothetical neural responses are shown in the middle two horizontal sections. "On" responses are at left, "off" responses at right. The difference between the "on" response to an additions and the "on" response to a contextual element is shown at bottom left. The difference between the "off" response to an addition and the "off" response to a contextual element is shown at bottom right. The shaded area represents the difference.

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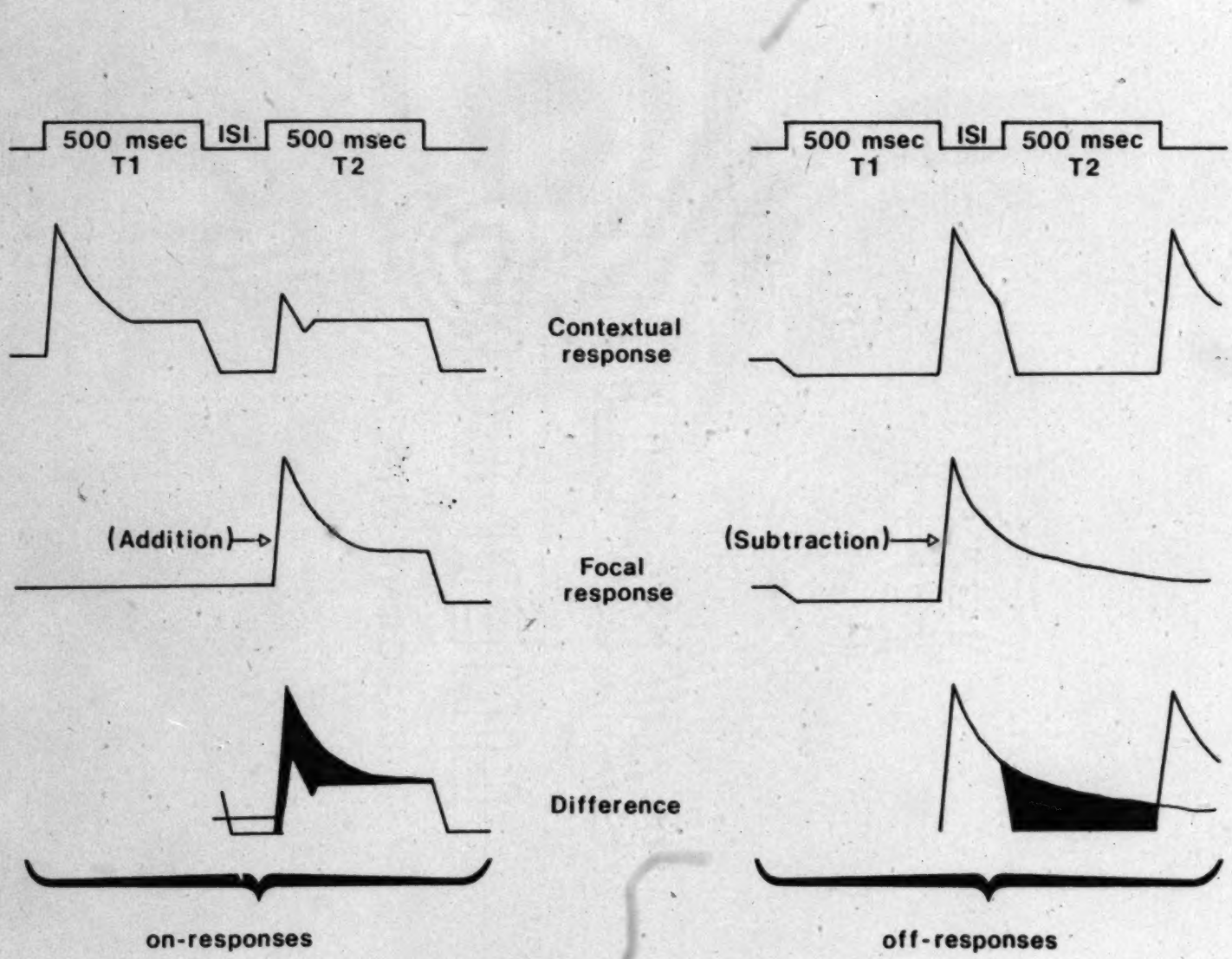
500 msec
T1
ISI
500 msec
T2
500 msec
T1
ISI
500 msec
T2
Contextual response
(Addition)
(Subtraction)
Focal response
Difference
on-responses
off-responses

response to each element reappearing in T2 is partially inhibited by its immediately preceeding "off" response . Only the addition (a new element) should produce a full-strength "on" response discriminable from the "on" responses of the reappearing elements. As the ISI increases and the inhibition of the "on" cells by the "off" cells dissipates, the "on" responses to reappearances regain their full strength and additions should become indiscriminable.

The "off" responses to each element at the offset of T1, which inhibit the "on" responses at the onset of T2, are themselves inhibited by these "on" responses. Only the subtraction, which does not reappear in T2 produces a full-strength "off" response which is discriminable from the off-reponses of reappearing elements. As the ISI increases, the "off" cells return to a base rate of activity before they can be inhibited by the "on" responses of T2, making subtractions indiscriminable from elements reappearing in T2.

Physiological support for the theory was provided by Singer and Phillips(1974). The work by Phillips and Singer(1974) and Singer and Phillips(1974) is exemplary for its successful convergence of neurophysiological and psychophysical methods to the study of the same theoretical issues. Using microelectrode recording techniques, Singer and Phillips(1974) studied "on" responses and "off" responses in X-type LGN cells of anaesthetized cats. A single spot of light focused onto the receptive field center

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of a cell provided the stimulus. The results of this research demonstrated that at short ISIs "on" responses to reappearances were reduced in amplitude compared to "on" responses to additions, and that "off" responses to elements terminating in T1 and reappearing in T2 were inhibited relative to "off" responses to subtractions. Thus, the physiological evidence was consistent with the theoretical explanation of performance in the psychophysical paradigm. [1]

Channels of information processing

Seven years after its publication the work of Phillips and Singer (1974) has been cited only twice (Coltheart, 1980, Long, 1980) in contexts which are only indirectly related to Phillips and Singer's (1974) and Singer and Phillips' (1974) original work. The lack of interest in their research may be due to a general lack of interest in "on" and "off" responses since the mid-1970s. The discovery of spatial frequency channels in the visual system by Campbell and Robson (1968) and the distinction between transient and sustained channels introduced by Cleland, Dubin and Levick (1971) may have shifted the attention of researchers and theorists away from "on" and "off" responses to spatial frequency channels and transient-sustained channels. Researchers have investigated the spatial

---

[1] In the remainder of this paper the terms "focal stimulus" or "focal element" are used to refer to the addition or the subtraction whenever a distinction between them is not necessary. The term "contextual elements" is used to refer to the elements continuing from T1 to T2. The corresponding terms, "focal response" and "contextual response(s)", are used to refer to the neural response produced by the elements.

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frequency tuning curves of cortical neurons (Albrecht, De Valois and Thorell, 1980), interactions between transient and sustained channels (Breitmeyer and Ganz, 1977; Von Grunau, 1978), temporal response properties of perceptual mechanisms tuned to separate ranges of spatial frequencies (Di Lollo and Woods, 1981), independence of spatial frequency channels (Graham and Nachmias, 1971), and relationships between transient-sustained channels and spatial frequency (Legge, 1978).

Research on spatial frequency channels suggests that the visual system possessses independent channels which are tuned to different frequencies. It is believed that these channels decompose the visual scene into its component frequencies (Pollen, Lee and Taylor, 1971). Along with spatial frequency channels it is currently believed that the visual system possesses transient and sustained channels. Transient channels are thought to process information about stimulus location and change of location or motion, while sustained channels process information about the spatial detail or form of the stimulus(Von Grunau, 1978).

The concept of a "channel" as it is exemplified by "spatial frequency channel" and "transient-sustained channel" can be defined as a visual pathway which transmits or processes some dimensions of a stimulus independently from other dimensions. This definition is implicit in the original usage by Campbell and Robson (1968) and is very similar to the definition of channel in theories of

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attention (Moray, 1970). Moray suggests that researchers interested in attention consider a dimension of an input message to be processed by an independent channel if the dimension can be selected by the subject. A channel need not refer to a particular anatomical structure, though it may(Nelson, Bartley, Bourassa,and Ball, 1971). However, it does imply a functional autonomy within the processing system, which means that input variations may affect one channel but not another.

Input to a channel may be either signal or noise. A signal is typically a focal stimulus, a target or probed item. Noise refers to the contextual stimulation, or anything which interferes with the detection of the signal. Generally, the greater the noise, or the weaker the signal (the smaller the signal-to-noise ratio), the more difficult the discrimination of the signal. Conversely, the weaker the noise, or the stronger the signal (the greater the signal-to-noise ratio), the easier the discrimination.

One method used to demonstrate the presence and independence of channels measures an observer's ability to select or detect the presence of a signal when the noise level in the hypothesized channel transmitting this signal is either high or low, and when the noise level in other irrelevant channels is either high or low. If the signal is accurately detected by the observer when the task-relevant channel is noise-free and other channnels have a high noise level, and if the signal is difficult to detect when the

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task-relevant channel has a high noise-level and other channels are noise free, a channel interpretation is consistent with the data. Typically, it is assumed that the signal and noise are processed by the same channel when they share some critical dimension.

Using the above method, the existence of independent information-processing channels may be inferred from at least three phenomena documented in the psychological literature: auditory shadowing, auditory masking, and visual masking.

In a shadowing task a subject is presented with two messages, one to each ear, and is required to repeat aloud one of the messages as it is being presented. The subject's success at discriminating the target message from the irrelevant message depends on the physical similarity between the two. Task difficulty increases as the message and voices of the speakers increase in similarity (Cherry, 1953).

In one version of auditory masking, the listener is presented with a test tone to one ear and a masking noise to the other. The task is to report the presence of the test tone. Performance is better when the test tone and mask are composed of different frequencies, than when the frequencies are similar (Zwislocki, 1978).

The third phenomenon that supports the notion of independent perceptual channels is visual masking. The observer is presented with a test target which is followed

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by a mask. The spatial frequency composition of the test target and mask are known. The observer's task is to report the presence of the test target. Performance is better when the test target and mask are composed of different frequencies than when the frequencies are similar (Stromeyer and Julesz, 1972). Thus, in each case, shadowing, auditory masking, and visual masking, some physical similarity between the signal and noise, or target and context, determines the ease of the task. In general, performance is better when the noise and signal differ.

The three phenomena suggest that an information processing system, whether visual or auditory, may contain various channels which are to some extent not overlapping. In the auditory and visual masking tasks different channels may process different frequencies, whereas information which has different voice quality may be processed by largely not overlapping channels in the auditory shadowing task. Furthermore, the phenomena suggest that each channel may have an independent noise level. When a signal occurs in a channel that is noise free, it is easily detected. When it occurs in a channel with a high level of noise it is difficult to detect.

Orientation of the present work

The research described in this thesis used a similar analysis. It suggested that "on" and "off" responses may be reconceptualized as separate processing channels. Experiment 1 replicated Phillips and Singer's (1974) original work and

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isolated a variable which could manipulate the noise level within the processing channels. Experiment 2 demonstrated how the noise level could be varied independently within the "on" channel and "off" channel and Experiment 3 manipulated the noise level in yet another manner. The present research also suggested that that the paradigm may be a useful tool to investigate rapid light adaptation.

Two modifications were introduced to the methodology used by Phillips & Singer (1974) to minimize the variability that might be introduced by decisional processes. Firstly, the yes-no method was replaced by a forced-choice method. Secondly, additions and subtractions were presented separately in blocks of 50 trials.

Methodological modifications

The yes-no method used by Phillips & Singer(1974), with blocked durations of T1, T2, ISI, and a random mixture of additions, subtractions and no-change trials has two inherent problems. The most serious is likely to have produced an internal inconsistency in the results of identical conditions of two separate experiments (Phillips and Singer, 1974, pp.499-500), which was entirely overlooked. Performance in the condition T1=2 msec, T2=500 msec, and ISI=100 msec was 85% correct for both additions and subtractions in one experiment and was much lower, approximately 50% correct, in another experiment. Fluctuations in the false alarm rate suggest that this is probably due to changes in the response criterion (i.e. the

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willingness of the observer to respond "yes"). The false alarm rate was near 40% in the experiment where performance was high, whereas it was near 0% in the experiment where performance was low. The high rate of false alarms may have inflated the number of correct detections in the experiment where performance was high. To surmount the problem of a fluctuating response criterion, a two alternative forced-choice method was adopted in this research, thus forcing the observer to set his or her response criterion at the theoretical maximum and respond "yes" on every trial.

The second problem concerns the random mixture of additions and subtractions within a block of trials. To detect a change, the observer must divide his or her attention between cues that signal an addition and cues that signal a subtraction. To minimize the possibility of an unequal division of attention, which could result in a difference in performance, additions and subtractions were blocked, so that a set of trials contained only additions or only subtractions.

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## II. Experiment 1

The first experiment followed closely the design of the original experiment conducted by Phillips and Singer(1974), but included the two methodological modifications just discussed. The aim of the experiment was to replicate the results obtained by Phillips and Singer (1974) and to test a variable which could affect the difficulty of the task by varying the noise level. The variable in question was the number of elements in the display, or density, which was manipulated to vary the noise level. It is assumed that the addition or the subtraction of the focal element is the signal or focal stimulus. The combined effect of all contextual elements in the display constitute the noise. The focal element should become difficult to discriminate as density increases, because the level of noise increases.

### A. Method

#### Procedure

The procedure outlined here was used in all three experiments. The display area (3°10'),element size (10') and minimal separation between elements (10') was the same as reported in Phillips and Singer(1974). The experiments were conducted at a photopic level of illumination (approximately 31.0 lux). Each element in the display was constructed from five closely packed luminous points. The elements were randomly scattered within the display area. Duration of T1 and duration of T2 were held constant at 500 msec. On each



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trial, two T1 - T2 pairs were displayed. The configuration of elements was randomly determined for each pair, and the number of elements (density) was fixed for a block of trials. There were 50 trials in each block, and each block contained only additions or only subtractions. Thus the maximum number correct is 50 and chance performance is equal to 25 correct responses.

The sequence of events on each trial was as follows: Four fixation dots appeared, one at each corner of the display, separated from the display area by 40′ of visual angle. The observer pressed the display button, the fixation dots dissappeared, and the first T1 - T2 pair was displayed. Five hundred msec after the display, the fixation dots reappeared. The observer pressed the display button again, the second T1 - T2 pair was displayed and the observer responded with button 1 or 2 to indicate whether the change occured in the first or second pair respectively. Observers were instructed to maintain a steady fixation throughout the display of each T1-T2 pair.

All scoring, timing and display functions were performed by a PDP-8/L computer. The display appeared on a Hewlett-Packard 1333A point plotter equipped with fast P15 phosphor. The display surface and surround were white, and the observer viewed the display from a fixed distance of 28 cm. The same three observers served in all three experiments. There were 50 trials for each condition of each experiment. The conditions were randomly ordered. Each

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experiment was replicated twice to increase statistical power. Thus, each observer had two sessions of each condition.

A calibration procedure insured that the luminous intensity of the oscilloscope was constant, given a constant Z-axis voltage (Di Lollo, 1979). To calibrate the oscilloscope, a test patch, consisting of a matrix of 19 x 19 dots spaced evenly in an area 9mm x 9mm in the center of the display surface, was plotted at a given Z-value, and refreshed every 10 msec. The luminance of the test patch was measured with a Tektronix J16 digital photometer equiped with a photosensitive probe reading in lux units. The lux scale was used in preference to the more appropriate nits scale, because the lux probe permitted greater resolution. The photometer was positioned at a distance of 28mm within a frame that hooked onto the face of the oscilloscope, excluding all extraneous light. The gain of the oscilloscope was adjusted so that a constant Z-axis voltage produced a constant reading on the photometer.

The refresh rate of the oscilloscope was set at 10 msec (100 Hz), well above the critical flicker frequency. The response of retinal ganglion cells to light flickering at rates greater than or equal to the critical flicker frequency is indistinguishable from that due to a steady light of the same energy as the mean value of the flickering light (Bishop, 1967; Ogawa, Bishop and Levick, 1966). Thus it is reasonable to assume that an intermittent display

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flickering at a rate above the critical flicker frequency and a steady display of the same energy as the mean value of the flickering display will affect the visual system identically. This is known as Talbot's law.

Design

In the first experiment the ISI between T1 and T2 was varied at seven levels:0, 10, 20, 40, 80, 160, 320 msec. Density was varied at three levels: 11, 21, 41 elements. The luminance of T1 and T2 did not vary, and was set to a comfortable intensity called low (L). The test patch plotted at this luminance produced a reading of 35 lux on the Tektronix J16 digital photometer.

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B. Results

Results of the first experiment are plotted in Figures 3, 4, and 5. The data were analyzed with a repeated-measures analysis of variance in which the factors were: density (11, 21 or 41 elements), ISI, additions v.s. subtractions, replication (first or second), and subjects (1-3). Observers improved from one replication of the experiment to the next, $F(1,2)=58.98$, $p<.02$, $MSe=1,157$. There was evidence of improvement at all ISIs except at an ISI of 0 msec, where performance was perfect, allowing for no improvement (replication x ISI interaction, $F(6,12)=3.43$, $p<.03$, $MSe=99$). (See Figure 3).

Figure 4 shows that density was a significant determinant of performance, $F(2,4)=270.82$, $p<.01$,

MSe=29,498. However, performance was perfect at an ISI of 0 msec regardless of density, and the effect of density was observed at ISIs greater than 10 msec, (density x ISI interaction, $F(12,24)=27.83, p<.01$, MSe=2,405).

Accuracy of performance decreased with increased ISI, $F(6,12)=64.33$, $p<.01$, MSe=11,515. Additions were easier to detect than subtractions, $F(1,2)=105.31$, $p<.01$, MSe=4,259. Subtractions showed a faster decline with increased ISI than did additions(additions-subtractions x ISI interaction, $F(6,12)=6.37, p<.003$, MSe=457), but the interaction between additions-subtractions and ISI was not identical at each level of density (additions-subtractions x ISI x density interaction, $F(12,24)=2.3$, $p<.04$, MSe=104). This can be seen in Figure 5, where the difference between additions and subtractions is approximately 2-3 correct at ISIs of 80 and 160 when density is 11 and 21 and near zero when density is 41.

C. Discussion

The results of Experiment 1 are in basic agreement with the data obtained by Phillips and Singer(1974). The two important features that are evident in Figure 1 are also evident in Figure 5. First, accuracy of performance decreased with increased ISI. Second, additions were easier to detect than subtractions. In general, the shapes of the functions obtained by Phillips and Singer(1974) and those obtained here are comparable, indicating that the

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Figure 3. Number of correct responses in Experiment 1 plotted as a function of the inter-stimulus interval between T1 and T2. Performance improved in the second replication of Experiment 1.

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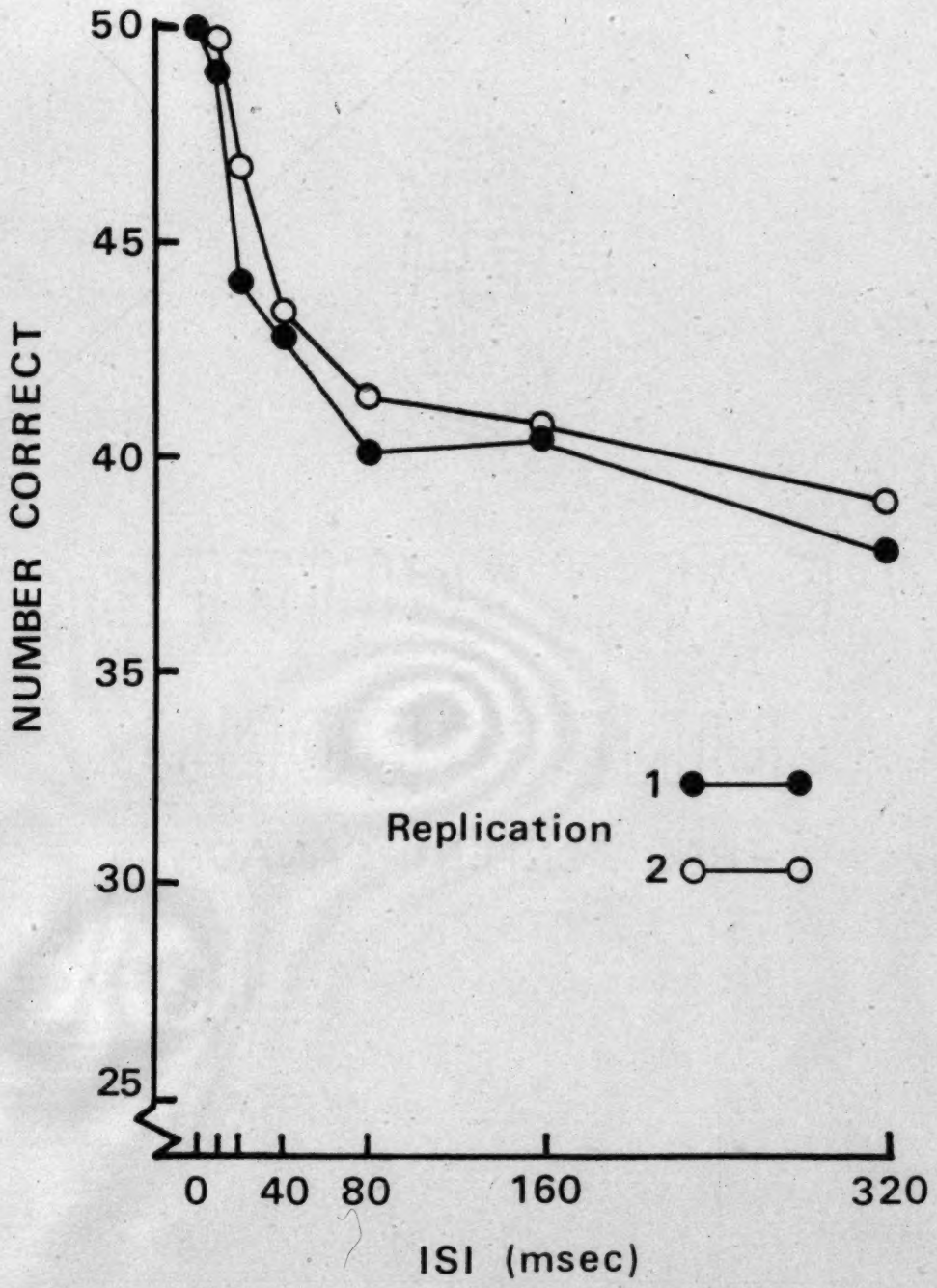
50
45
40
35
30
25
NUMBER CORRECT
1
Replication
2
0
40
80
160
320
ISI (msec)

Figure 4. Number of correct responses in Experiment 1 plotted as a function of the inter-stimulus interval between T1 and T2. The curves for densities 21 and 41 have two segments: one extending to approximately 80 msec and the other to 320 msec. The effect of density is evident.

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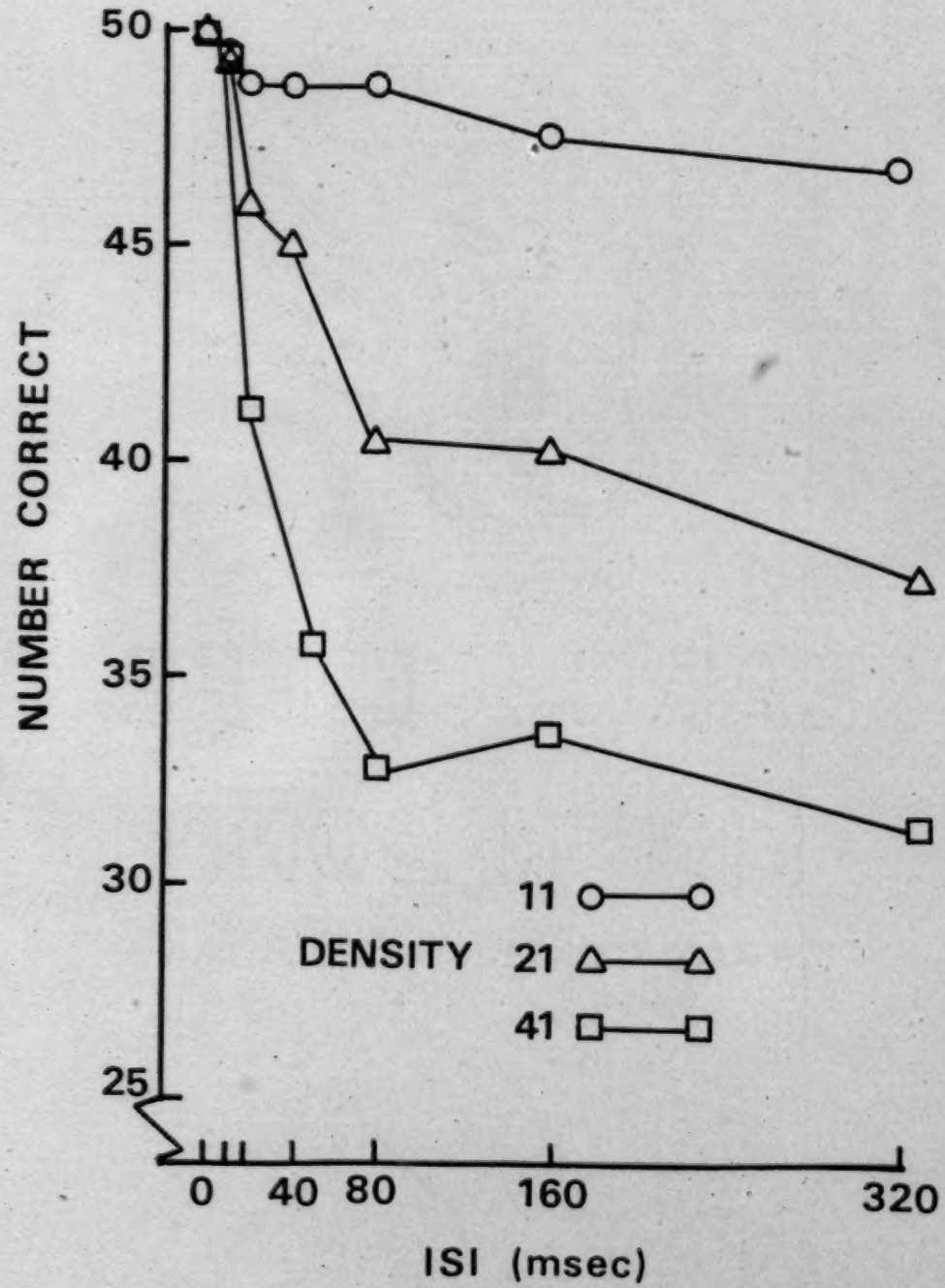
50
45
40
35
30
25
NUMBER CORRECT
11
DENSITY 21
41
0
40
80
160
320
ISI (msec)

Figure 5. Number of correct responses for additions and for subtractions in Experiment 1 plotted as a function of the inter-stimulus interval between T1 and T2, separately for each level of density.

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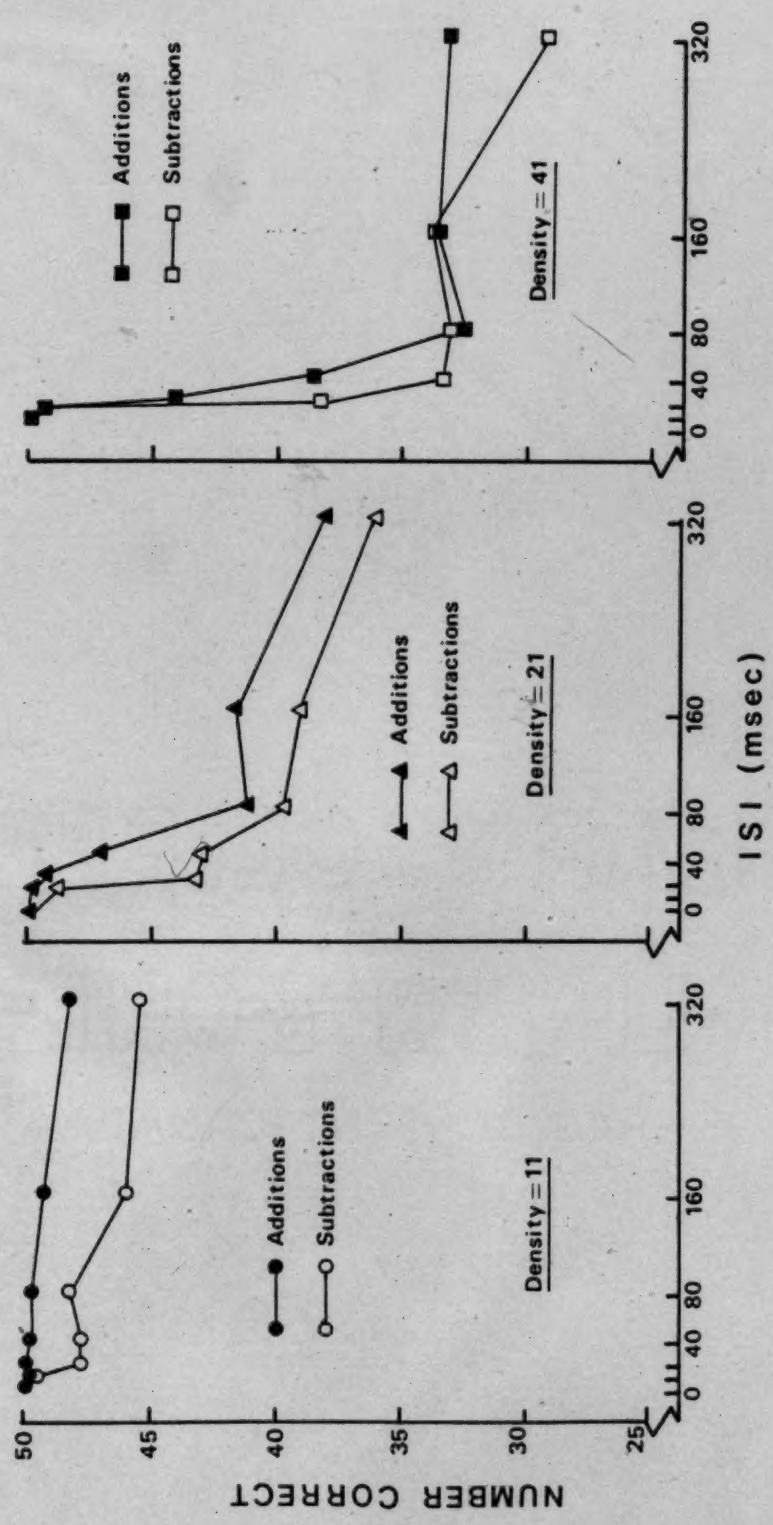
NUMBER CORRECT
50
45
40
35
30
25
Density = 11
Additions
Subtractions
Density = 21
Additions
Subtractions
Density = 41
Additions
Subtractions
0
40
80
160
320
ISI (msec)

replication was successful.

One feature of the results, however was not consistent with Phillips and Singer's(1974) and Singer and Phillips' (1974) theory. According to Phillips and Singer (1974) inhibitory effects of the "on" and "off" responses which mediated performance in those conditions of Experiment 1 where the ISI was greater than 0 msec are expected to dissipate at long ISIs. Thus, performance is expected to eventually reach chance level i.e., 25 correct responses. The duration of ISI at which the inhibitory effects should dissipate in the human visual system is not clear,although it is probably less than 320 msec and possibly less than 160 msec. In the curarized cat with a stimulated mecencephalic reticular formation, inhibitory effects were negligible after approximately 280 msec, and were at 20% of maximum by approximately 180 msec (Singer and Phillips, 1974). If we were to use these values as broad estimates of the time course of inhibitory events in the human visual system, we would expect performance to reach chance level by 320 msec, whereas Figures 4 and 5 clearly show that performance is well above chance for all three densities at this ISI. This suggests that performance was mediated by an alternate mechanism at long ISIs. Some durable form of memory or abstract representation of T1 and T2 may well be responsible.

A closer examination of the data suggests that the explanation proposed by Phillips and Singer(1974) is

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appropriate at short ISIs, where inhibitory mechanisms are likely to be operating, and a different explanation is appropriate for ISIs outside the temporal limit of the inhibitory effects.

Ignoring for the moment the curves for the lowest density, note that the curves in Figures 4 and 5 appear to have two segments: one segment with a steep slope extending approximately to 80 msec, followed by a segment with a shallow slope. The distinct change in the slope suggests that the mechanism mediating performance may be different in the two segments. To maximize performance, observers may have employed a different basis of judgment at long ISIs than at short ISIs. The inflection in the curves in Figures 4 and 5 may indicate the point where they switched the basis of judgment, and where the advantage of using one basis over the other reversed.

The mechanism mediating performance in the first segment would require a rapidly changing state to explain the steep slope, whereas the opposite should be true of the mechanism mediating performance in the second segment. The inhibitory mechanism suggested by Phillips and Singer(1974) fits the prerequisites for the first segment of the curve, because the inhibition produced by the "on" and "off" responses is short lasting, and a more durable form of memory fits the prerequisites for the second segment. Thus, the explanation of peformance proposed by Phillips and Singer(1974) may apply to the first portion of the curves in

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Figures 4 and 5, and a different explanation, possibly invoking a durable memorial representation, applies to the second portion of the curves. Of major interest to the present work is the early portion of the curves in Figures 4 and 5.

Density

As expected, density had a pronounced effect on performance. As density increased performance deteriorated, though only when associated with an ISI greater than 10 msec. The effect of density is evident within both segments of the curves in Figure 4 for densities 21 and 41. In the curve representing performance in the lowest density condition in Figure 4 a steep initial segment is missing or is very short, extending to an ISI of only 20 msec. This suggests that performance at this density was mediated primarily by one mechanism, possessing very similar characteristics to the mechanism which mediated performance at densities 21 and 41 at long ISIs. Apparently, a configuaration of 11 elements was easier to remember than a configuration of 21 or 41 elements so as to overshadow the inhibition at ISIs greater than 20 msec. Presumably, the advantage of using changes in configuration to detect the focal element decreased as density increased, explaining the observers' preference to use the information provided by inhibitory mechanisms at short ISIs with densities 21 and 41.

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The difference in performance among the three densities at long ISIs may reflect the ease of remembering the configuration of elements in the display. A configuration containing few elements is notably easier to remember, than a configuration of many elements. The number of elements in a display is an adequate indicator of the complexity of the configuration only when the elements are presented in a random configuration.The number of elements would not be an appropriate indicator of complexity if a more regular pattern were available (Kaufman, 1974; Wertheimer, 1923).

The difference in performance among the three densities at short ISIs may reflect variations in the noise level of the detection mechanism. In the absence of an understanding of the detection mechanism it is difficult to specify the exact nature of the noise; nevertheless one can speculate on its nature. If the detection mechanism must scan the display, increasing density may change the efficiency of this scan. Alternatively if the information in the display is compressed at later stages of processing, increasing density may change the efficiency of the process which performs the compression, or transmits the compressed information.

In summary, at extremely low densities, performance may be mediated by a durable memorial representation of the display over the entire range of ISIs, whereas within a middle range of densities, performance is more likely to be determined primarily by sensory factors at short ISIs, and

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by a memorial representation at long ISIs. Furthermore, at short ISIs, varying density within a middle range of densities is more likely to affect the noise level of the detection mechanism rather than change the picturability of the pattern of elements in the display.

Phillips and Singer (1974) and Singer and Phillips (1974) were also aware of the possibility that bases of judgment might vary with density. However, they were interested in the inhibitory interactions of "on" and "off" responses in overlapping receptive fields of LGN cells and thus their theory is restricted to describing neural activity produced by individual elements in the display. A display of one element or one hundred elements is equivalent according to their theory. Nevertheless, the display used by Phillips and Singer (1974) contained 50 elements on average. The choice of 50 elements in their psychophysical experiment was obviously based on extratheoretical grounds. According to the authors, a high density minimized the likelihood that observers were basing their judgments on an abstract representation of pictorial structure and increased the likelihood that they were basing their judgments on the detection of onsets and offsets. Results from Experiment 1 are consistent with this reasoning.

An alternative explanation of the effect of density within the initial segment of the curves might suggest that density is not a unidimensional variable. Two dimensions are readily apparent: number and proximity. Figure 6 presents

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two photographs, a photograph of a 21-element display, and a photograph of a 41-element display. Note that the absolute number of elements and the average proximity between the elements are confounded with each other: as one increases, the other also increases. Either or both could account for the effect of density observed in Experiment 1. Varying the number of elements may well vary the noise level, however varying the proximity may vary the strength of the focal response or the signal. As the proximity between the elements increases the likelihood that they will interact with each other may also increase. If these interactions are inhibitory, this may affect the strength of the focal response or signal. There are several neurophysiological findings that are compatible with an inhibitory explanation of the effect of density. Inhibitory interactions between LGN cells with different receptive fields have been found in the visual system of the cat (Derrington and Fuchs, 1979). Furthermore, research on lateral inhibition suggests that inhibition increases as the proximity between neural elements decreases. For example, in the Limulus, eye inhibitory interactions are detectable between adjacent neurons, and virtually undetectable between neurons that are further apart from each other (Hartline, Wagner and Ratliff, 1956).

In a low density condition, the elements in the display are relatively well spaced. In a high density condition the elements are closely packed. Thus, inhibitory spatial

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Figure 6. Photographs of typical displays. A display with 21 elements is shown at top and one with 41 elements is shown at bottom.

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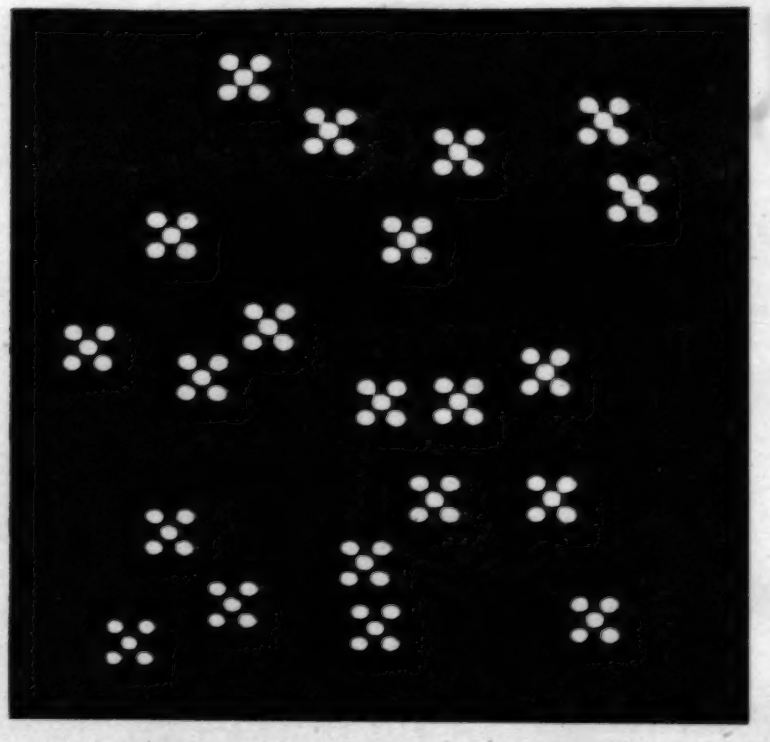

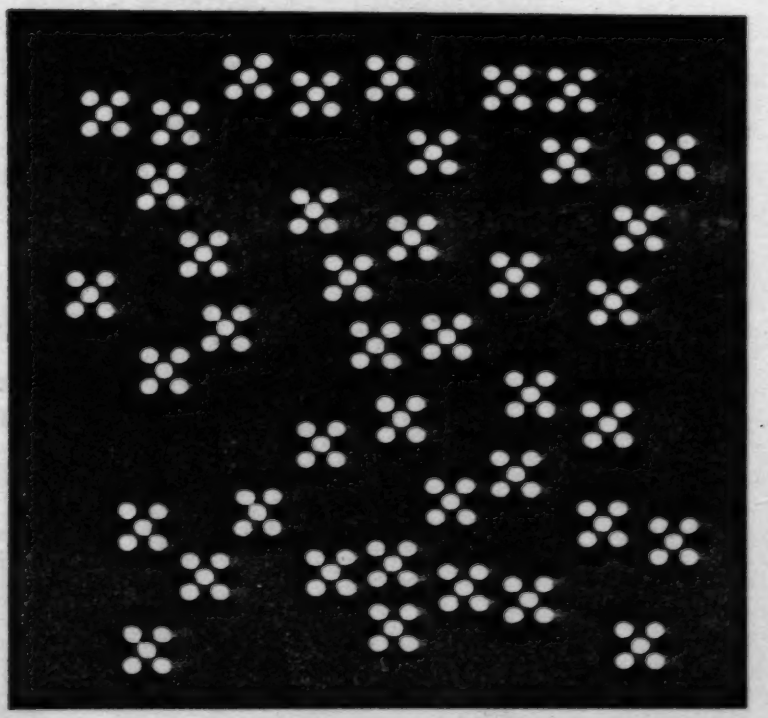

interactions are likely to be stronger in a high density condition than in a low density condition. If the "on" response to the addition were selectively inhibited by the neighboring "on" responses occuring at the onset of T2, then the response to the addition would be stronger in a low density condition than in a high density condition. Since, according to Phillips and Singer(1974), the discriminability of the addition is directly dependent on the difference in intensity between the "on" response produced by the addition and the "on" responses produced by the contextual elements, discriminability of the addition should be poorer in the high density condition than in the low density condition. Similarly, if the "off" response to the subtraction were selectively inhibited by the neighboring "off" responses occuring at the offset of T1, then the response to the subtraction would be stronger and thus easier to discriminate in a low density condition, than in a high density condition.

In general the inhibitory explanation of the effect of density suggests that the strength of the focal response or signal varies as density increases. The discrimination becomes difficult as density increases because the focal element produces a weaker response.

The two explanations of the effect of density, the inhibitory explanation and the noise level explanation, may both be true. They are logically compatible with each other, and the mechanisms suggested by each are largely

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independent. Variations in density could conceivably affect either or both mechanisms. The inhibitory explanation of the effect of density, however is unlikely to be true for two reasons.

One problem with this explanation is the requirement that the neural response to the focal element be selectively inhibited, or inhibited proportionately more than the neural responses to the contextual elements. Selective inhibition is necessary, because a proportional or constant change in the size of the focal and contextual responses would not explain how the prominence of the focal element decreases as density increases. This requirement goes beyond the available neurophysiological evidence and runs counter to some evidence from the Limulus eye. In the Limulus eye the amount of inhibition is independent of the strength of the response of the ommatidium that is being inhibited (Hartline, Wagner, and Ratliff, 1956). If this is also true for the human visual system, then a mechanism which could select the focal response and inhibit it proportionately more than the contextual responses may not be available.

The other problem is the time course of inhibition. When dealing with lateral inhibition, the time course of the inhibitory process must be considered (French, 1979). If, as Phillips and Singer (1974) suggest, the detection of the focal element is based on early response activity in the visual system, then lateral inhibition may not have time to act, and may have no effect on performance. These problems

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suggest that an explanation of the effect of density in terms of lateral inhibition is likely to be untenable.

Two more features of the data from Experiment 1 merit discussion. First, faultless performance at an ISI of 0 msec and second, differential performance on additions and subtractions.

Performance at ISI=0 msec

Perfect performance at an ISI of 0 msec is consistent with both explanations of the density effect. In the absence of an ISI, the focal element was the only element in the display which produced a response at the transition from T1 to T2. The contextual elements appeared continuous throughout the entire 1000 msec display, and did not produce responses at the transition from T1 to T2. Thus, the level of noise, which is determined by the response to the contextual elements, should have been zero, and inhibitory interactions should have been impossible. Consequently, the signal to noise ratio should have been very high, and the detection of the focal element easy. This is indeed what the results show.

Performance on additions and subtractions

The remaining issue concerns the difference between performance on additions and subtractions. Additions were easier to detect than subtractions in both segments of the curves in Figure 5. The advantage of additions over subtractions however, varied with ISI. The difference was maximal at an ISI of 20 msec and 40 msec, and minimal at

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long ISIs. This quantitative difference in performance provides further support for the argument that different mechanisms are necessary to explain performance in each segment of the curves in Figures 4 and 5.

Phillips and Singer(1974) suggested that the detection of subtractions was more difficult than the detection of additions because the difference between the "off" response to a subtraction and the "off" responses to the contextual elements is smaller than the difference between the "on" response to the addition and the "on" responses to the contextual elements. Note in Figure 2 that the difference between the "off" responses is restricted to the tail of the response, whereas the difference between the "on" responses includes the entire response. This explanation is plausible, but applies only to the initial segment of the curves in Figure 5, where antagonistic inhibition is operating.

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## III. Experiment 2

Experiment 1 replicated Phillips and Singer's (1974) experiment and demonstrated an effect of density. Under certain conditions increasing density was thought to increase the noise level in the detection mechanism. Experiment 2 attempts to vary the noise level of "on" and "off" channels independently. If "on" and "off" responses can be reconceptualized as independent or largely not overlapping processing channels in the visual system, it should be possible to show that the noise level can be varied independently in each channel.

In the paradigm used in Experiment 1, and in Phillips and Singer(1974), subtractions occurred at the termination of T1, and additions at the onset of T2. This meant that subtractions always occurred in the context of "off" responses and additions always occurred in the context of "on" responses. In experiment 2 the paradigm was modified to allow all four combinations of additions and subtractions with contextual "on" and "off" responses. The ISI was omitted. In its place, a sudden shift in the level of luminance was introduced at the transition from T1 to T2. A shift from a low luminance level in T1 to a high luminance level in T2 (LH) was expected to produce an "on" response in the "on" cells, whereas a shift from a high luminance level in T1 to a low luminance level in T2 (HL) was expected to produce an "off" response in the "off" cells. The addition or subtraction occurred simultaneously with the shift in



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luminance. A schematic representation of the paradigm is presented in Figure 7. The conditions where the focal response and contextual responses were both "on" responses or both "off" responses are henceforth referred to as "same context" conditions.The conditions where the focal response and contextual responses were different, one an "on" response and the other an "off" response, are henceforth referred to as "different context" conditions.

Predictions of performance can be derived from an explanation which considers "on" and "off" responses as occuring in independent channels. According to this explanation, performance should be better in the "different context" conditions, (additions with contextual "off" responses and subtractions with contextual "on" responses) because an increment in luminance would increase the noise level in the on-channel in the LH condition leaving the off-channel largely unaffected, so that the "off" response to a subtraction would occur in a relatively noise-free channel. Similarly, a decrement in luminance would increase the noise level in the off-channel in the HL condition leaving the on-channel largely unaffected, so that the "on" response to an addition would occur in a relatively noise-free channel. Thus the focal element should be easily detected in the "different context" condition and should be difficult to detect in the "same context" condition.

Consider now variations in denity. Since variations in density should vary the level of noise primarily in the

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Figure 7. A schematic representation of the paradigm used in Experiment 2. The luminance shift from T1 to T2 is either from high to low or from low to high. The addition or the subtraction occurs simultaneously with the shift in luminance. There is no inter-stimulus interval between T1 and T2.

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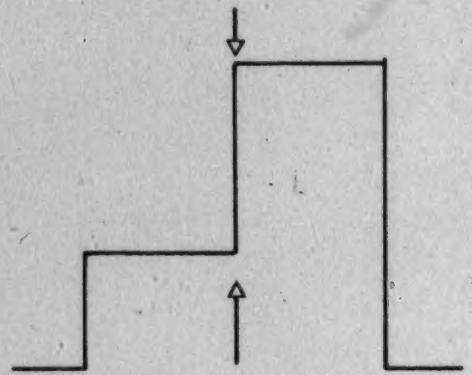
Low to High
(LH)

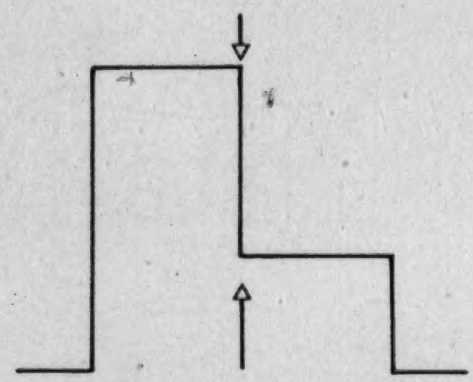
addition or subtraction occurs here



contextual on-responses

High to Low
(HL)

addition or subtraction occurs here



contextual off-responses

on-channel in the LH condition, and in the off-channel in the HL condition, the effect of density should be evident primarily in the "same context" condition, where the signal occurs in the channel with the high level of noise. Thus performance should decrease at a higher rate as density increases in the "same context" condition than in the "different context" condition. In a nutshell, the results of Experiment 2 should show a main effect of context and an interaction between context and density.

A. Method

The paradigm used in Experiment 1 was modified in the following manner: The ISI was fixed at 0 msec and replaced with a sudden shift in the level of luminance at the transition from T1 to T2. The shift was from a high to a low level of luminance (HL) , or from a low to a high level (LH). The high level of luminance was defined as the level at which the intensity test patch (see page 19) produced a reading of 312 lux on the Tektronix J16 digital photometer. Similarly, the low level of luminance produced a reading of 35 lux. Five levels of density were investigated: 11, 16, 21, 31, and 41 elements. As in Experiment 1, durations of T1 and T2 were constant at 500 msec each. Two control conditions:low to low(LL) and high to high (HH) were also included. The control conditions insured that variations in performance that might emerge in conditions LH and HL could not be attributed to differences in absolute luminance of

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the display but rather to the transition in luminance from T1 to T2.

B. Results

The results of Experiment 2 are plotted in Figures 8, 9, and 10. The data were analyzed with a repeated measures analysis of variance in which the factors were: context ("same" or "different"), density (11, 16, 21, 31, 41) additions v.s. subtractions, replication (first or second), and subjects (1-3). Performance was near ceiling at the lowest density and declined progressively as density increased, $F(4,8)=79.69$, $p<.01$, $MSe=311$. The rate of decline was greater in the "same" context, than in the "different" context, $F(4,8)=17.4$, $p<.05$, $MSe=104$. (See Figure 8). The main effect of context was marginally significant, $F(1,2)=14.49$, $p=.06$, $MSe=1197$. A Neuman-Keuls test showed that the main effect of context was significant at densities 21, 31 and 41 ($p<.01$).

Additions were generally easier to discriminate than subtractions, (main effect of additions-subtractions was marginally significant, $F(1,2)=10.58$, $p=.08$, $MSe=525$). (See Figure 9). The two-way interaction between additions-subtractions and density was significant, $F(4,8)=6.06$, $p=.015$, $MSe=25$ (Figure 9). This interaction appeared to be primarily due to the performance ceiling at the lowest density. A simple-effects test of the interaction of additions-subtractions and density at densities 21, 31,

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Figure 8. Number of correct responses in Experiment 2 plotted as a function of the density of the elements in the display. Performance was better in the "different" context conditions than in the "same" context conditions. The effect of density is evident primarily in the "same" context condition.

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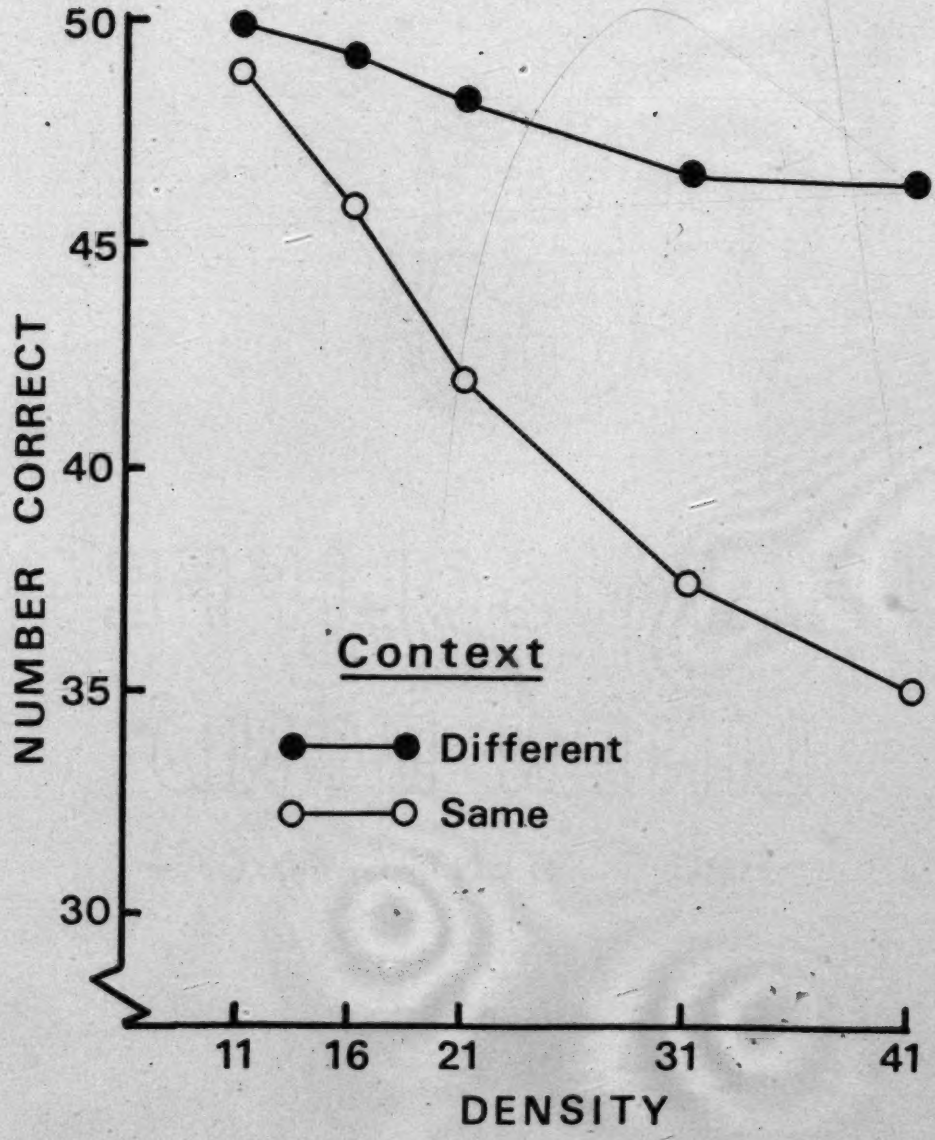
50
45
40
35
30
NUMBER CORRECT
Context
Different
Same
11
16
21
31
41
DENSITY

Figure 9. Number of correct responses in Experiment 2 plotted as a function of the density of the elements. Additions were easier to detect than subtractions.

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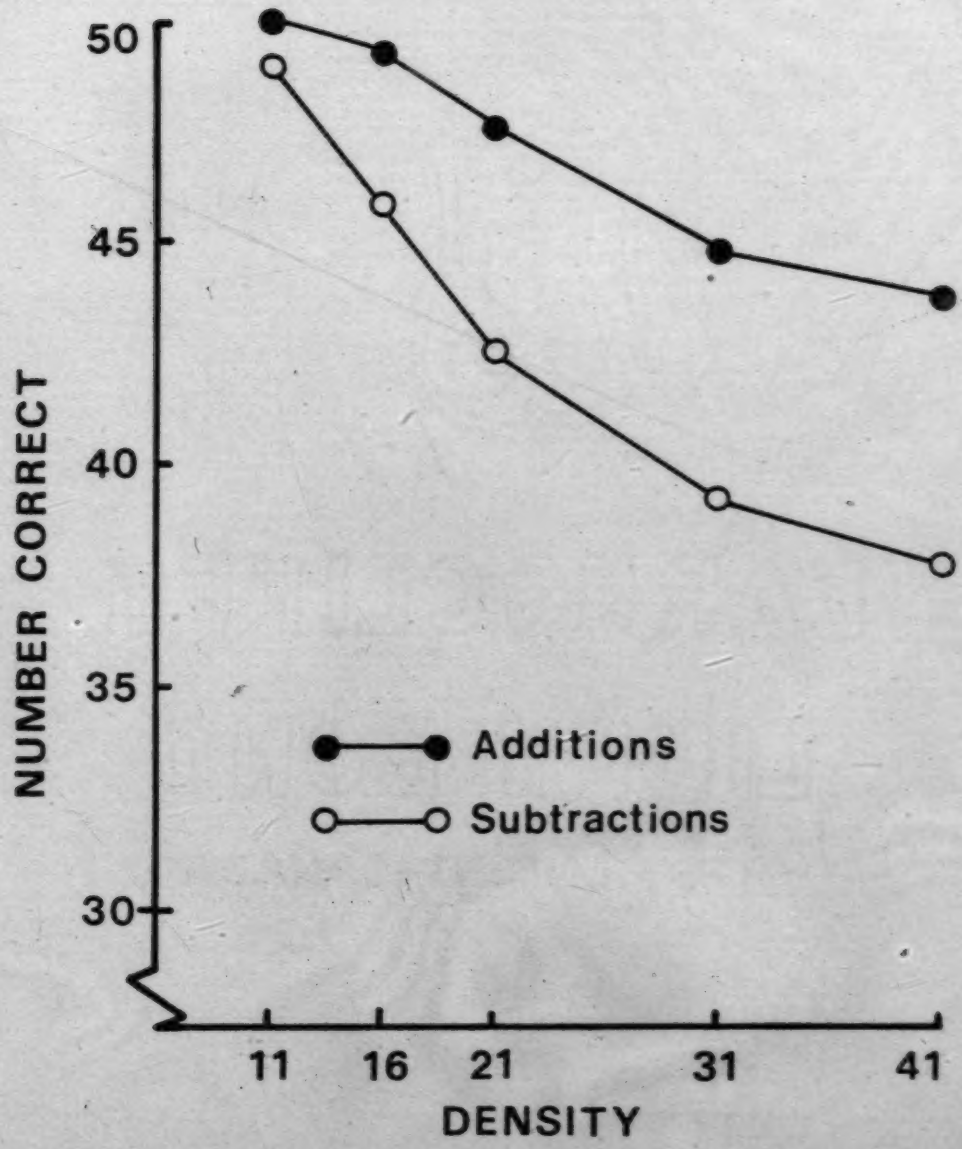
50
45
40
35
30
NUMBER CORRECT
Additions
Subtractions
11
16
21
31
41
DENSITY

Figure 10. Number of correct responses in Experiment 2 plotted as a function of the density of the elements, separately for additions (10a) and for subtractions (10b).

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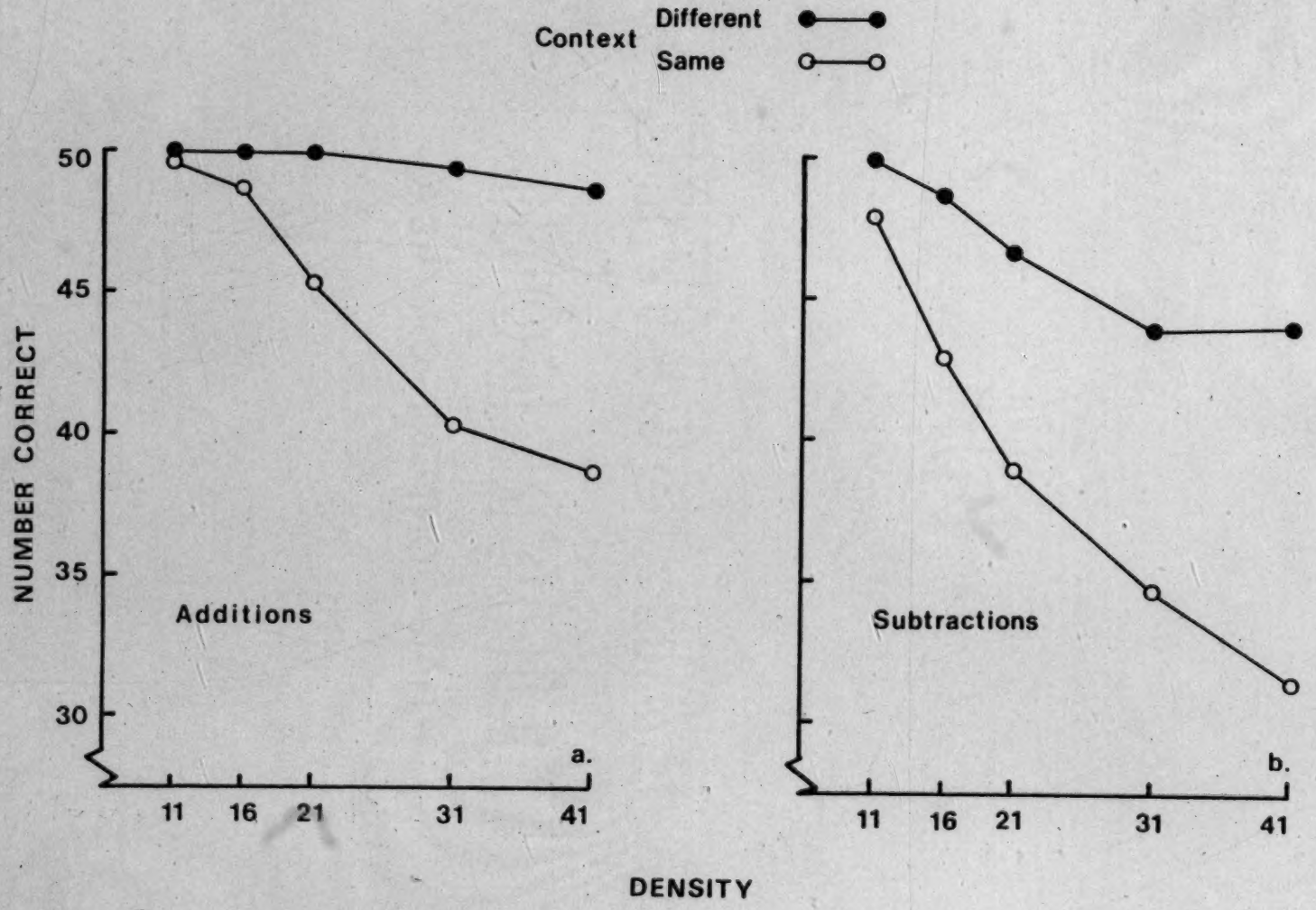
Context
Different
Same
NUMBER CORRECT
50
45
40
35
30
Additions
a.
11
16
21
31
41
Subtractions
b.
11
16
21
31
41
DENSITY

41 was not significant, $F(2,8)=.311$, $MSe=1.29$, suggesting that the difference between additions and subtractions, at densities 21, 31, and 41 was approximately constant. The three way interaction between additions-subtraction, density, and context was not significant, $F(4,8)=.89$, $MSe=3$. (See Figure 10). Performance was faultless in the two control conditions, LL and HH.

C. Discussion

The results of Experiment 2 were consistent with a view that "on" and "off" responses may be conceptualized as independent processing channels in the visual system. In general, performance was higher when the focal response occurred in a context that was "different" than when it occurred in a context that was the "same". First, additions which produce "on" responses, were difficult to detect in the context of "on" responses and were easier to detect in the context of "off" responses(Figure 10a). Subtractions which produce "off" responses, were difficult in the context of "off" responses, but were easier in the context of "on" responses(Figure 10b). Second, the effect of the context interacted with the effect of density(Figure 8). Performance declined as density increased, but the rate of decline was critically dependent on the nature of the contextual stimulation or the noise. Increasing density caused performance to drop more when the focal and contextual stimuli were qualitatively similar than when they differed.

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These results are consistent with a view that distinguishes between two processing channels: the on-channel and the off-channel. Increasing density appeared to increase the level of noise primarily in the on-channel in the LH condition and primarily in the off-channel in the HL condition. Since the focal response occurred in the low-noise channel in the "different context" condition and in the high-noise channel in the "same context" condition, performance was lower in the "same context" condition and the effect of density was evident primarily in the "same context" condition.

Other aspects of the data from Experiment 2 also merit discussion, specifically, the relationship between Experiments 1 and 2, the difference between additions and subtractions, and the bases of judgment used in Experiment 2.

Validity of the comparison of experiments 1 and 2

Apparent methodological differences between experiments 1 and 2 do not preclude comparison of their results. From the observers' perspective, the task in both experiments was very similar. It required the detection of a focal element in the context of other elements. The focal element was either an onset (addition) or offset (subtraction). From a theoretical perspective, the focal element was detectable in both experiments because its neural response was stronger than the responses to the contextual elements. In Experiment 1, at short ISIs, the response to the focal element was

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stronger because the temporal interactions between "on" and "off" cells inhibited the responses to the contextual elements, but not to the focal element. In Experiment 2 the response to the focal element was stronger because the luminance shift of the focal element was always greater than the luminance shift of the contextual elements. Since the size of the increment or decrement in luminance determines the size of the neural response(DeValois, Jacobs, and Jones, 1962), and since the focal element always appeared from zero luminance (addition) or dropped to zero luminance (subtraction), whereas the luminance shift of the contextual elements was always a proportion of the luminance shift of the focal element, the focal element always produced a stronger response. Therefore, it appears that the basis for detecting the focal element was similar in experiments 1 and 2 and a comparison of the two experiments is warranted.

Additions and subtractions

Additions were easier to detect than subtractions in Experiments 1 and 2. Phillips and Singer(1974) suggested that additions were easier because the basis for detecting an addition included the entire response, whereas only the tail of the response was available for detecting a subtraction, as can be seen in Figure 2. In Experiment 2 the detection of both additions and subtractions was based on the entire response, and this is diagrammed in Figure 11. The shaded areas in Figure 11 represent the hypothetical differences in response amplitude between the focal and

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Figure 11. The paradigm used in Experiment 2 is presented schematically at the top of the figure. The dotted line represents the luminance shift of the focal element. Hypothetical neural responses to the contextual elements and focal element are shown in the middle two horizontal sections. "On" responses are at left, "off" responses at right. The difference between the "on" response to an addition and the "on" response to a contextual element is shown at bottom left. The difference between the "off" response to a subtraction and the "off" response to a contextual element is shown at bottom right. The shaded area represents the difference.

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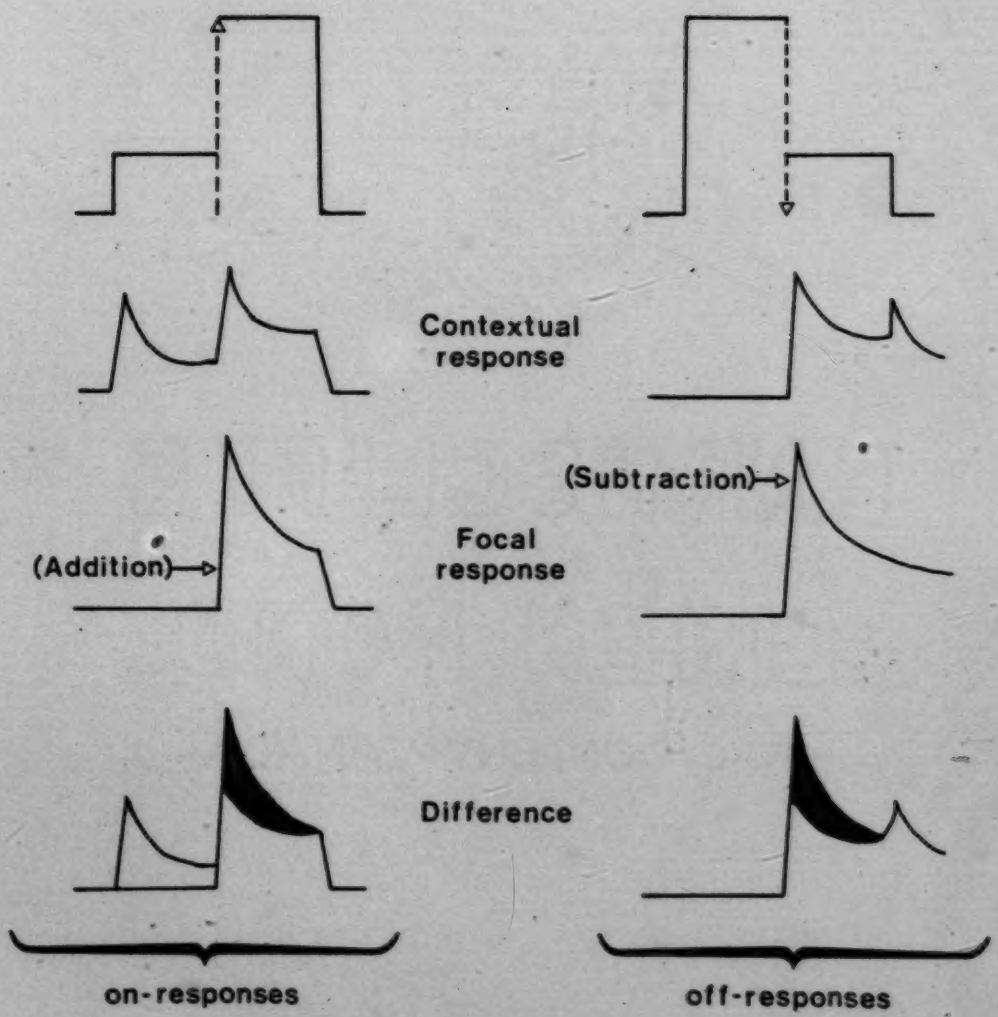
Contextual response
(Addition)
Focal response
(Subtraction)
Difference
on-responses
off-responses

contextual elements. The shaded areas are identical for additions and subtractions in Figure 11, whereas they differ in Figure 2. If Phillips and Singer's (1974) argument is true, we would expect additions and subtractions to be detected with equal accuracy in Experiment 2, because the basis for the detection was identical. Additions however, remained easier(Figure 9). Therefore, the explanation proposed by Phillips and Singer(1974) for the difference between the the detectability of additions and subtractions was not supported in Experiment 2.

Rapid, local light adaptation of the retina provides a more likely explanation of the difference between additions and subtractions. Rapid light adaptation of the retina has a latency of less than 100 msec and is believed to be neurally mediated (Uttal 1973, Crawford,1947, Baker,1963, Dowling, 1967). As the luminance level increases, the sensitivity of the visual system decreases because the adaptation level of the retina increases (French, 1979; Jacobs, 1965; Stevens and Stevens, 1963). Thus, if two stimuli of identical luminance were presented, one to a light-adapted retinal area and one to a dark-adapted retinal area, the neural response to the latter would be more intense. [2]

Given these assumptions one can draw the following inferences. In experiments 1 and 2 the retinal areas stimulated by the elements in the display should have a

---

[2] Adaptation might occur at many levels of the visual system. In this thesis the term "adaptation" refers to local, rapid, retinal adaptation.

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higher adaptation level and lower sensitivity than the areas that were unstimulated and remained adapted to the background luminance. Thus, a subtraction must always occur on a retinal area that is preadapted and has a lower sensitivity than the retinal area where an addition must occur. Since the luminance shifts of the addition and of the subtraction were constant at 35 lux in Experiment 1, and were constant at 312 lux in Experiment 2, the response of the visual system to the subtraction must be smaller than to the addition. Consequently, the subtraction should be more difficult to detect.

A fundamental assumption made by the preceeding explanation of the difference between additions and subtractions is that eye movements did not occur for at least 100 msec (the presumed course of neural adaptation) before the end of T1. Clearly, retinotopic alignment of T1 with T2 would be violated if observers moved their eyes during the display of a T1-T2 pair. Observers were instructed to maintain a constant fixation throughout the display of each T1-T2 pair, however, eye-movements were not monitored in the experiments. In cases where eye-movements did occur, it is assumed that they occured randomly and that they did not introduce any systematic bias into the results. These assumptions regarding eye-movements are maintained throughout this thesis.

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Bases of detection, or bases of judgment

It is unlikely that changes in configuration or changes

in number of elements were used as bases for detecting the focal element in Experiment 2. Observers are accurate at subitizing the number of elements in brief random displays of elements only when there are fewer than six or seven elements(Kaufman, Lord, Reese, and Volkmann, 1949).In Experiment 2 performance was at ceiling when 11 elements were presented in the display, more than could be subitized accurately.

It may be noted that the overall configuration formed by the elements in T1 changed at the transition from T1 to T2 when an element was added or subtracted. It is possible that observers used such change in overall configuration to detect the focal element. This is most likely to have happened at densities 11 and 16 where where the small number of elements facilitated detection of configurational changes. This was suggested earlier (see page 29) in the discussion of the results of Experiment 1. In Experiment 1 performance at the lowest density (11) did not exhibit an initial rapid decline as the ISI increased. This was considered to be indicative of a detection strategy based on changes in configuration. At higher densities, however, performance did show an initial steep decline. This was considered to be indicative of a detection strategy based on differences in response amplitude to focal and contextual elements. It is likely that differences in response amplitude were also present in Experiment 2. Given the observers' preference to use these differences for detecting

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the focal element, at densities 21 and 41 in Experiment 1, it is likely that the same basis of detection was used at densities 21, 31 and 41 in Experiment 2.

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## IV. Experiment 3

Experiment 2 presented evidence consistent with a view that "on" and "off" responses may be conceptualized as independent processing channels. Specifically, that the noise level in the two channels could be varied independently by varying density. Experiment 3 attempts to vary the noise level in the two channels by varying the size of the luminance shift from T1 to T2. It may be noted that the size of the neural response of the visual system is directly related to the size of the luminance shift (De Valois, Jacobs, and Jones, 1962).

In Experiment 2 the luminance of T1 and T2 was always at one of two levels: high or low. The high level was the maximal luminance output of the display unit and produced a reading of 312 lux on the Tektronix J16 digital photometer. The low level produced a reading of 35 lux. Consequently, at the transition from T1 to T2 the contextual elements always shifted 277 lux, from 312 to 35 or from 35 to 312. Experiment 3 varied the size of the shift parametrically.

Predictions of performance in Experiment 3 are similar to those in Experiment 2. The focal element should be easier to detect in a "different context" condition than in a "same context" condition, and the effect of increasing noise by increasing the size of the luminance shift should be evident primarily in the "same context" condition.

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A. Method

In Experiment 3 the density was constant at 41 elements. The size of the luminance shift from T1 to T2 was varied. Initially, four intermediate levels of luminance were selected to partition the range between 35 lux and 312 lux into five segments. Later, extra levels were added to avoid extensive extrapolation between data points. In the initial selection, logarithmic units rather than arithmetic units were deemed to be more appropriate, because the response of visual system is believed to be roughly proportional to the logarithm of the intensity (DeValois, Jacobs & Jones, 1962). The following values of lux were selected: 35, 38, 45, 64, 124, 312. The additional lux levels were: 85, 147, 201, 259.

Two variations of the low to high shift conditions, and two variations of the high to low shift conditions were used. See Figure 12 and 13 for a schematic representation of these conditions. The shifts from T1 to T2 in Figures 12 and 13 are not drawn to scale. In one variation the shift was always initiated from 312 lux or always terminated at 312 lux(Figures 12a and 13a). In this variation the LH shifts were: 312-312, 124-312, 64-312, 45-312, 38-312, 35-312(Figure 12a); the HL shifts were: 312-312, 312-124, 312-64, 312-45, 312-38, 312-35(Figure 13a). The additional lux levels were not necessary in this variation because extensive extrapolation between the data points was unnecessary. In the second variation the shift was always

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Figures 12 and 13. A schematic representation of the "same" context conditions used in Experiment 3. The shifts in luminance from T1 to T2 are not drawn to scale. The dotted line represents an addition in Figure 12 and a subtraction in Figure 13. In Figures 12a and 13a the luminance of either T1 or T2 is fixed at 312 lux, and in Figures 12b and 13b it is fixed at 35 lux. The symbols to the right of the figures correspond to the symbols used in Figures 14a and 15.

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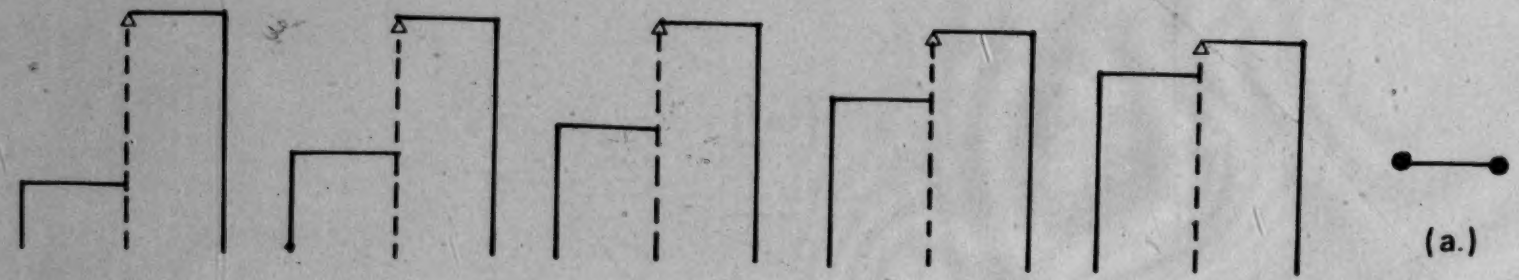
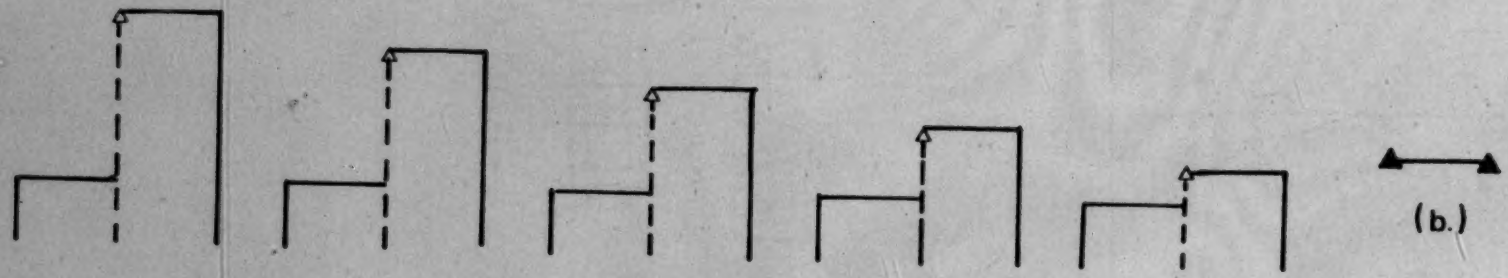
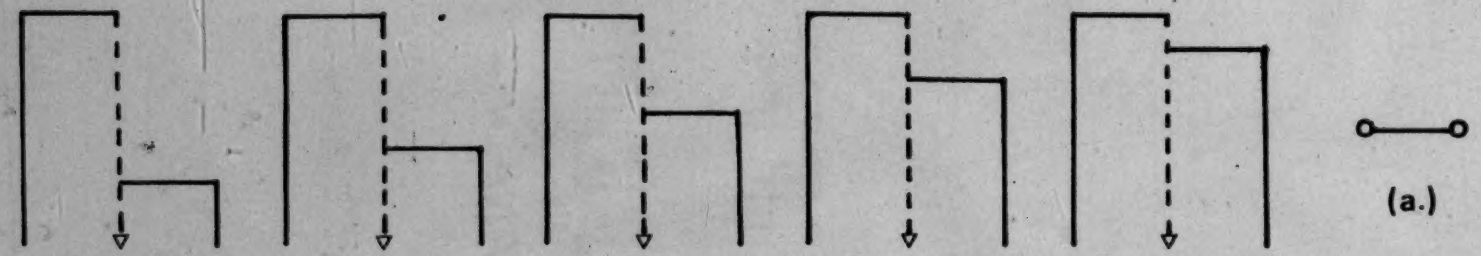


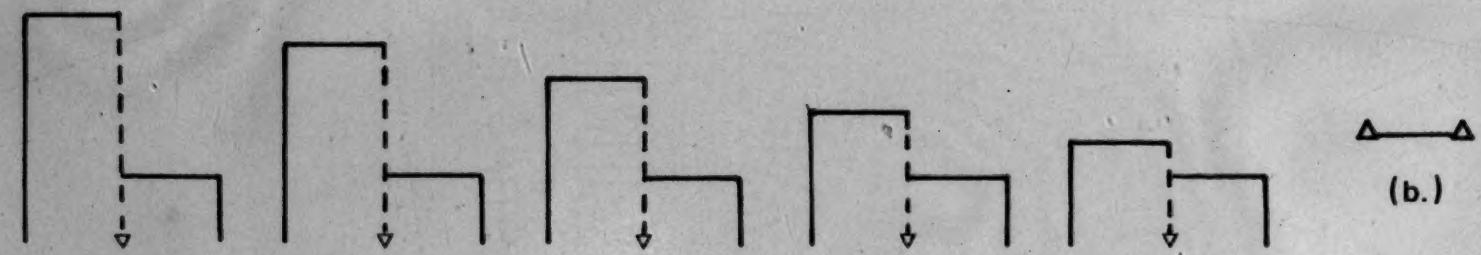

Additions – T2 fixed at 312 lux (T1 varies)




Additions – T1 fixed at 35 lux (T2 varies)




Subtractions – T1 fixed at 312 lux (T2 varies)




Subtractions – T2 fixed at 35 lux (T1 varies)

initiated from 35 lux or always terminated at 35 lux (Figures 12b and 13b). In the second variation the LH shifts were:35-35, 35-38, 35-45, 35-64, 35-85, 35-124, 35-147, 35-201, 35-259, 35-312(Figure 12b); the HL shifts were:35-35, 38-35, 45-35, 64-35, 85-35, 124-35, 137-35, 201-35, 259-35, 312-35 (Figure 14b). The additional lux levels were used in this variation to avoid extensive extrapolation between the data points and thus there are 4 more data points in HL and LH in the second variation than in the first.

B. Results and Discussion

Results from Experiment 3 are presented in Figures 14, 15, and 16. Performance in Figure 14 is plotted as a function of the size of the luminance shift of the contextual elements i.e., the shift between T1 and T2. For example, when the luminance of T1 was 35 lux and the luminance of T2 was 147 lux, the shift between T1 and T2 was 112 lux.

The results of Experiment 3 are clearly consistent with the view that "on" and "off" responses may be conceptualized as independent processing channels. The focal element was easier to detect in the "different context" condition than in the "same context" condition (Figure 14b vs. Figure 14a), and the effect of increasing the size of the luminance shift was evident primarily in the "same context" condition (Figure 14a). Performance deteriorated as the size of the

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Figure 14. Number of correct responses in Experiment 3 plotted as a function of the size of the luminance shift from T1 to T2, separately for the "same" context condition (14a) and separately for the "different" context condition (14b). Performance decreased as the size of the shift of the contextual elements increased.

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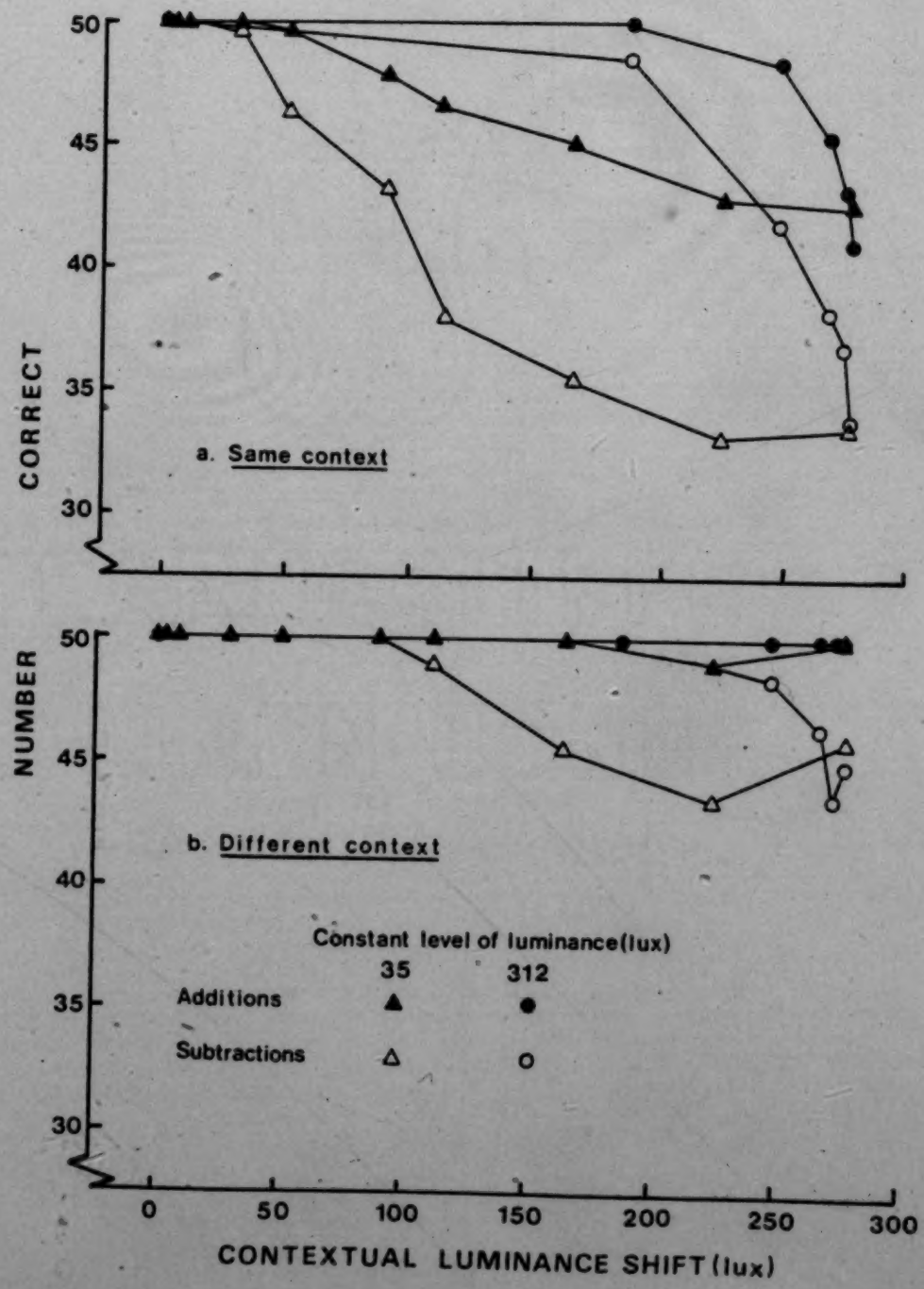
50
45
40
35
30
CORRECT
a. Same context
NUMBER
b. Different context
Constant level of luminance(lux)
35
312
Additions
Subtractions
0
50
100
150
200
250
300
CONTEXTUAL LUMINANCE SHIFT (lux)

Figures 15 and 16. Number of correct responses in Experiment 3 plotted as function of the ratio of the luminance shift (focal to contextual), separately for the "same" context condition (Figure 15), and for the "different" context condition (Figure 16). Performance increased as the size of the ratio increased.

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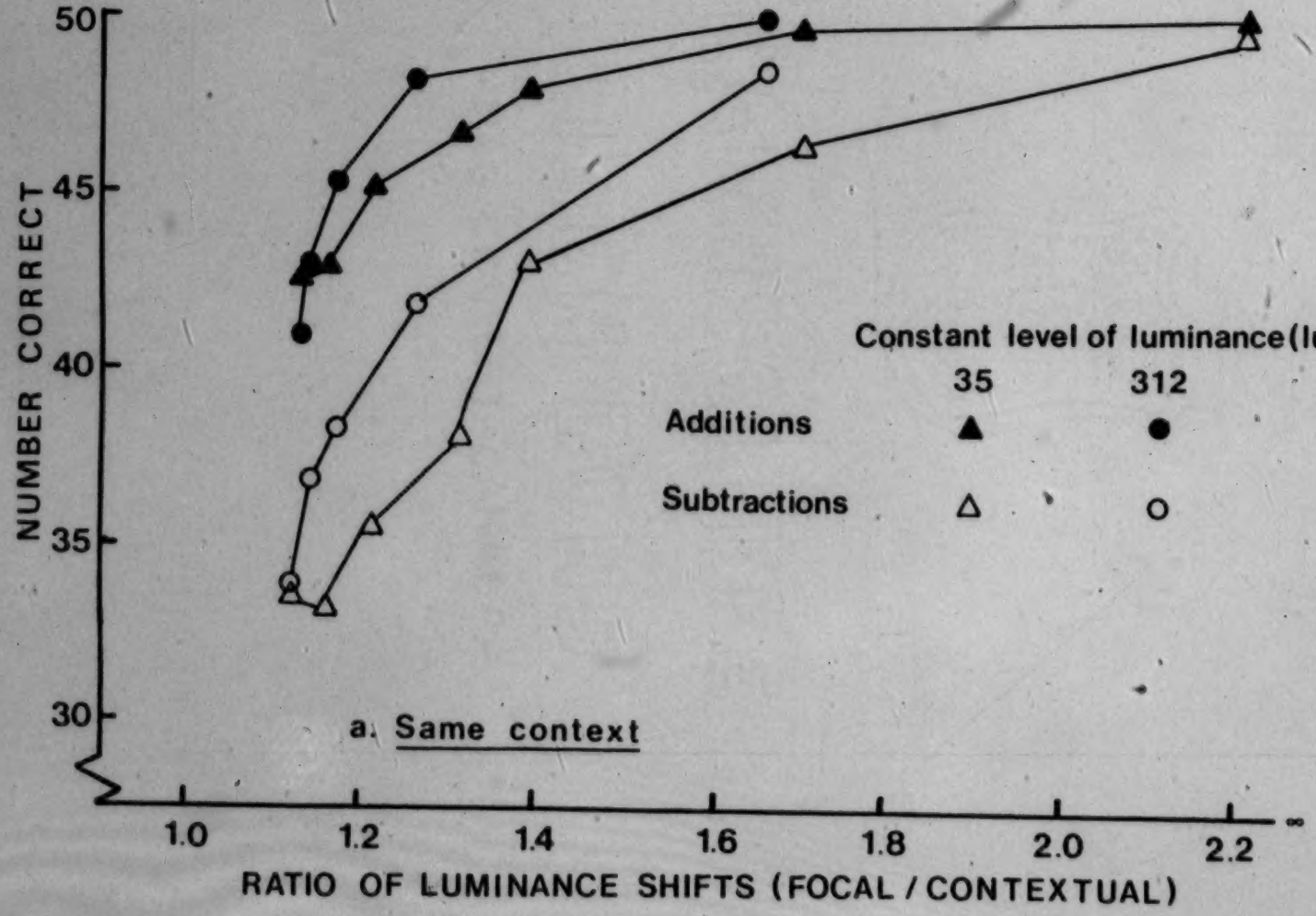
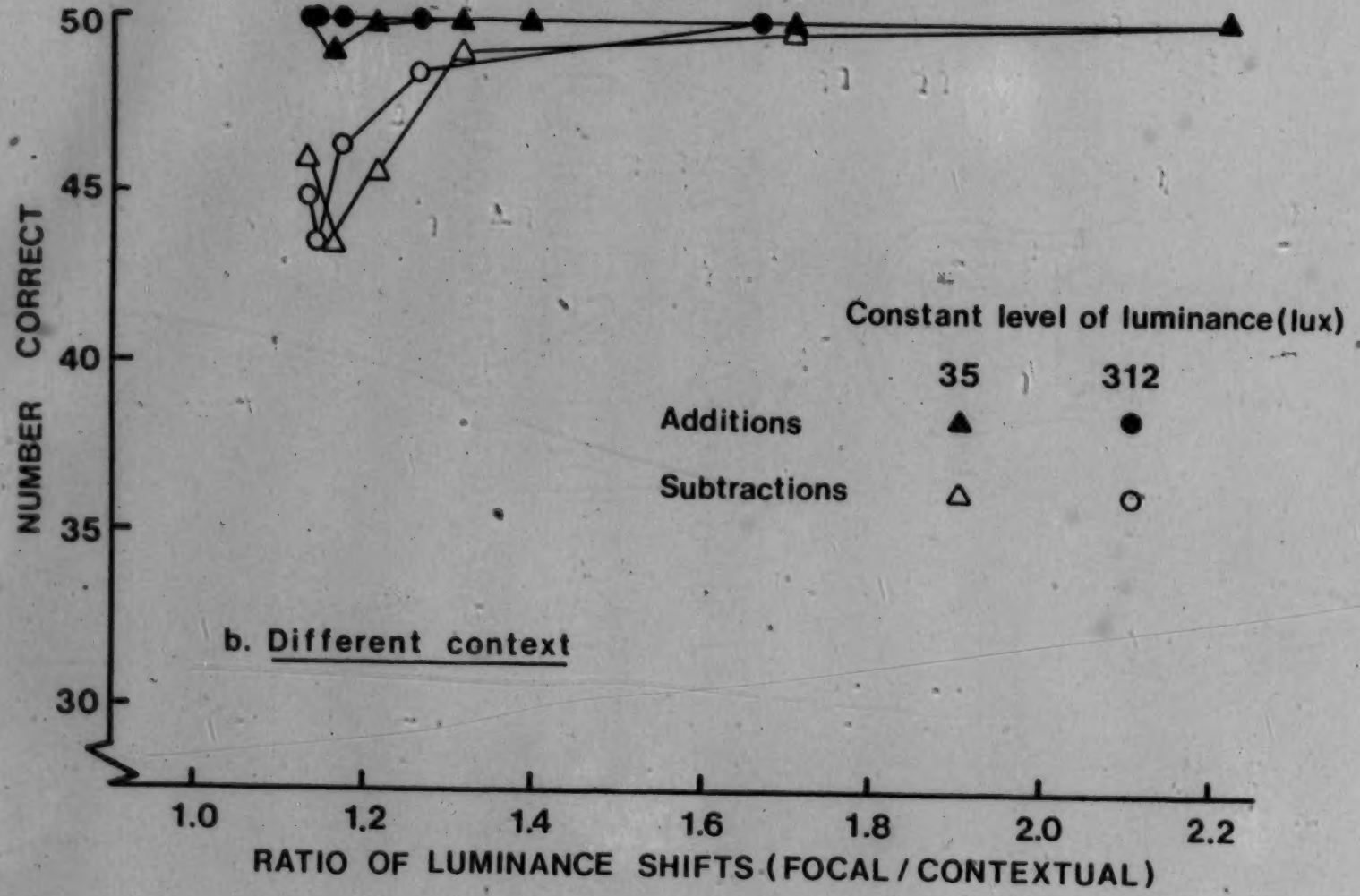

50
45
40
35
30
NUMBER CORRECT
Constant level of luminance (lux)
35
312
Additions
Subtractions
a. Same context
1.0
1.2
1.4
1.6
1.8
2.0
2.2
∞
RATIO OF LUMINANCE SHIFTS (FOCAL / CONTEXTUAL)


50
45
40
35
30
NUMBER CORRECT
Constant level of luminance(lux)
35
312
Additions
Subtractions
b. Different context
1.0
1.2
1.4
1.6
1.8
2.0
2.2
RATIO OF LUMINANCE SHIFTS (FOCAL / CONTEXTUAL)

shift increased. Consistent with Experiments 1 and 2, additions were easier to detect than subtractions.

Other patterns which emerged in the data from Experiment 3 are also interesting. Except at the maximal shift and at shifts where performance was at ceiling, observers detected the focal element more accurately in conditions where T1 or T2 were constant at 312 lux. In Figure 14, this difference in performance appears as a difference between open circles and open triangles (subtractions), and between filled circles and filled triangles (additions). Both in the case of additions and in the case of subtractions performance was very similar at the maximal shift (277 lux), regardless of the level at which T1 or T2 were held constant, because the shifts were identical. The shifts were from 35 to 312 lux or from 312 to 35 lux.

To understand the difference in performance between conditions where 312 lux was constant and conditions where 35 lux was constant, it is necessary to realize that the luminance levels of T1 and T2 determine the size of the luminance shift of the focal element, as well as the size of the luminance shift of the contextual elements. The size of the shift of the contextual elements is determined simply by the size of the shift from T1 to T2. The size of the shift of the focal element is determined differently for additions and for subtractions. For additions, the size of the shift is determined by the luminance level of T2, because additions rise from the background luminance to the

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luminance level of T2. For subtractions, the size of the shift is determined by the luminance level of T1, because subtractions drop from the level of T1 to the background luminance. The dotted lines in Figures 12 and 13 represent the luminance shift of the focal element for the "same context" condition.

Consider first the divergence between the filled circles and filled triangles (additions) in Figure 14a. The filled circles represent performance on additions where T1 varied and T2 was constant at 312 lux (Figure 12a). The filled triangles represent performance on additions where T1 was constant at 35 lux and T2 varied (Figure 12b). Since the size of the luminance shift of the addition was determined by T2, the size of the addition was always 312 lux for the filled circles and less than 312 lux for the filled triangles, except at the maximal shift. Note that the dotted lines are shorter in Figure 12b compared to Figure 12a at all shifts except the maximal shift.

Consider next the divergence between the open circles and open triangles (subtractions) in Figure 14a. The open circles represent performance on subtractions where T1 was constant at 312 lux and T2 varied (Figure 13a). The open triangles represented performance on subtractions where T1 varied and T2 was constant at 35 lux (Figure 13b). Since the size of the luminance shift of the subtraction was determined by the level of T1, the size of the luminance shift of the subtraction was smaller for the open triangles

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than for the open circles, except at the maximal shift. Note that the dotted lines are shorter in Figure 13b compared to Figure 13a at all shifts except the maximal shift. It is likely that the divergence between the open circles and open triangles and between the filled circles and filled triangles in Figure 15a is due to differences in the size of focal shift. Performance is lower in conditions represented by the triangles, because the focal shift is smaller in these conditions than it is in the conditions represented by the circles for any given shift of the contextual elements, except the maximal shift. This explanation also applies to Figure 14b, which presents data from conditions where the focal and contextual shifts differed. The focal shift was smaller in the conditions represented by the triangles than in conditions represented by the circles, and thus performance was lower in these conditions.

In the discussion of Experiment 2 it was considered unlikely that observers perceived a change of configuration at densities 21, 31, and 41, or used this as a basis for detecting the focal element. The results of Experiment 3 provide further support for this argument. They suggest that the sizes of the contextual shift and focal shift jointly determined the prominence of the focal element. The larger the shift of the focal element and the smaller the shift of the contextual elements, the greater was the prominence and detectability of the focal element.

A convenient expression of the relative size of the

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focal and contextual shifts is a ratio of the two shifts, focal to contextual. Manipulating the size of the shift of either the focal element or the contextual elements affects the ratio systematically. The limiting cases of the ratios are, at one extreme, when there is no shift in the contextual elements and the shift of the focal element is maximal, and at the other, when the shifts of the focal and contextual elements are equal to each other. In the first case, the ratio is infinitely large and in the second, it is equal to one. Performance should improve as the ratio increases from one to infinity. The data of Experiment 3, which are plotted in Figure 14, are replotted as a function of the ratio of focal to contextual shifts in Figure 15 for the "same context" condition and in Figure 16 for the "different context" condition. Consistently with our expectations performance in Figures 15 and 16 can be seen to improve as the ratio increases.

The ratio of the focal to contextual shift is an accurate representation only of the distal stimulus, i.e. the physical stimulus. To determine whether a focal stimulus was or was not present, the decisional system of the observer does not use the ratio of the luminance shifts in the distal stimulus, but, possibly, a ratio of the neural responses produced by the luminance shifts. If the ratios of the luminance shifts corresponded exactly to the ratios of neural responses produced by these shifts, the curves in Figure 15 would be superimposed and so would the curves in

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Figure 16. The fact that they are not superimposed suggests that the strength of the neural responses do not match faithfully the magnitudes of the luminance shifts. However, the noncorrespondence is systematic, as indicated by the fact that the filled circles lie above the filled triangles, the open circles lie above the open triangles, and the filled symbols lie above the open symbols in Figure 15. The pattern of performance is similar in Figure 16. The divergence between the curves can be explained in terms of rapid light adaptation.

Consider first the divergence between the filled symbols in Figure 15. The filled triangles represent performance on additions where the luminance of T1 was fixed at 35 lux and T2 varied, and the filled circles represent perfomance on additions where the luminance of T2 was fixed at 312 lux and T1 varied. These conditions are represented schematically in Figure 12, and the corresponding symbols are located to the right of the Figure. At points where the filled circles and filled triangles diverge in Figure 15, the adaptation level induced by T1 was higher in the conditions where T2 was fixed at 312 lux (filled circles) relative to the conditions where T1 was fixed at 35 lux (filled triangles). This is shown in Figure 12. Note that the luminance levels of T1 are higher in Figure 12a than in Figure 12b for all luminance shifts except the maximal shift. The divergence between the filled symbols in Figure 15 may be due to differing levels of adaptation. The higher

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the level of adaptation, the lower the sensitivity. Consequently, the sensitivity of the retinal locations stimulated by the contextual elements was lower in conditions represented by the filled circles relative to the filled triangles because the adaptation level in the conditions represented by the filled circles was higher. Thus, the contextual response per equal shift in luminance of the contextual elements was smaller in conditions represented by filled circles than in conditions represented by filled triangles. The corresponding ratios of neural responses (focal to contextual) was presumably larger for filled circles than for filled triangles given equal ratios of luminance shifts. We may assume that the adaptation level of the inter-element spaces where the addition occurred was constant. Thus, it can be said that the ratios of the luminance shifts of conditions represented by filled circles underestimate the ratios of neural responses relative to conditions represented by filled triangles. Consequently, we would expect filled circles to diverge from filled triangles when plotted as a function of the ratio of luminance shifts. The filled circles should be displaced towards smaller ratios of luminance shifts relative to the filled triangles in Figure 15. The divergence of filled circles from filled triangles in Figure 15 is consistent with these expectations.

Consider next the divergence between subtractions represented by open circles and open triangles in Figure 15.

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The adaptation level of the contextual elements determined by the luminance level of T1 was higher in conditions represented by the circles. Compare Figure 13a to Figure 13b. Note that the adaptation level induced by the luminance of T1 is higher in the conditions where T1 is fixed at 312 lux (open circles), than it is in conditions where T2 is fixed at 35 lux (open triangles), except at the maximal shift. As in the case of additions (filled symbols), the divergence between subtractions (open symbols) can be ascribed to differing levels of adaptation. The sensitivity of the retinal locations stimulated by the contextual elements was lower in conditions represented by open circles relative to open triangles because the adaptation level was higher in conditions represented by open circles. Thus the neural response per equal shift in luminance of the contextual elements was presumably smaller in the conditions represented by open circles, than in conditions represented by open triangles. Therefore, the corresponding ratios of neural responses (focal to contextual) were probably larger for open circles than for open triangles per equal ratio of luminance shifts. Thus, it can be said that the ratios of luminance shifts of conditions represented by open circles underestimate the ratios of neural responses relative to conditions represented by open triangles. Consequently we would expect open circles to be displaced towards smaller ratios of luminance shifts relative to filled triangles in Figure 15. The pattern of results in Figure 15 confirms our

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expectations.

The adaptation level of the retinal location where the subtraction occurred may have affected the divergence of the curves representing performance on subtractions in Figure 15. The sensitivity of the retinal location of the subtraction is likely to have been higher for conditions represented by open triangles relative to open circles, because the luminance of T1 was lower for conditions represented by open triangles (see Figure 13). Thus the neural response to the subtraction per equal shift in luminance was probably higher in conditions represented by open triangles, than open circles. Therefore, the corresponding ratios of neural responses (focal to contextual) were probably larger for open triangles relative to open circles. This would tend to minimize the divergence between subtractions in Figure 15. However the divergence between subtractions does not appear to be smaller than the divergence between additions.

Consider finally the divergence between additions and subtractions in Figure 15. The adaptation level of the retinal location of the addition was lower than the adaptation level of the retinal location of the subtraction because the retinal location of the addition was adapted to the background luminance of the display, whereas the retinal location of the subtraction was adapted to the luminance of T1. Therefore the sensitivity of the retinal location of the addition was higher than the sensitivity of the retinal

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location of the subtraction, and the focal response per equal shift in luminance was probably smaller for subtractions than for additions. In turn, the corresponding ratios of neural responses (focal to contextual) per equal ratio of luminance shifts were probably larger for additions than for subtractions. Thus, it can be said that the ratios of luminance shifts of additions underestimate the ratios of neural responses relative to subtractions. Consequently in Figure 15 we would expect the filled symbols to be displaced towards smaller ratios of luminance shifts relative to the open symbols. The pattern of results in Figure 15 confirm these expectations.

In summary, the ratios of the luminance shifts (focal to contextual) do not correspond exactly to the ratios of the neural responses produced by these shifts. It is suggested that the noncorrespondence can be adequately explained by differences in the level of adaptation induced by T1. Specifically, that a luminance shift of a constant magnitude may produce a neural response whose magnitude is determined in part by the adaptation level of the retina. The divergence between the curves in Figure 15 can be attributed to the fact that the adaptation level induced by T1 is not considered when plotting the data as a function of the ratio of the luminance shifts (focal to contextual).

The preceeding discussion of performance in the "same context" condition represented in Figure 15 can also be applied to performance in the "different context" condition

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represented in Figure 16. The pattern of results in Figure 16 is similar to the pattern observed in Figure 15 and can also be explained in terms of adaptation. The divergence between open and filled symbols (subtractions and additions respectively) can be ascribed to differing levels of adaptation of the retinal locations of additions and subtractions. The divergence between filled symbols (additions) is small and probably due to chance. The divergence between open symbols (subtractions) can be ascribed to differing adaptation levels induced by T1. The luminance of T1 and the contextual luminance shifts are represented schematically for the open symbols in Figure 12a and for the open triangles in Figure 12b. The symbols in Figure 12 correspond to the "same context" condition (Figure 15) and do not correspond to the"different context" condition (Figure 16).

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## V. General Discussion

The present research explored the psychophysical paradigm developed by Phillips and Singer (1974). The paradigm was extended by systematically varying the density of the elements, by replacing the ISI with a luminance shift and by varying the size of the shift. The results can be summarized as follows: performance deteriorated as the ISI between T1 and T2 increased; additions were easier to detect than subtractions; performance deteriorated as density increased; the focal element was difficult to detect in a "same context" and easy to detect in a "different context"; performance was poorer the lower the adaptation level of T1. In general, the results were consistent with Phillips and Singer's (1974) results and with the main aspects of their explanation.

The primary goal of the research was to demonstrate the independence of on and off-channels in the visual system. The results of Experiments 2 and 3 were consistent with a view that "on" and "off" responses can be reconceptualized as virtually indepenent channels. These results can be contrasted with those obtained by Phillips and Singer (1974) who suggested that "on" and "off" responses were strongly interdependent and inhibited each other when they occurred in overlapping receptive fields. If we can assume that the elements in the displays used here stimulated largely nonoverlapping receptive fields then it appears that "on" and "off" responses from different receptive fields do not



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inhibit each other but, quite the contrary, they appear to be processed by separate channels. Thus, in general, "on" and "off" responses of nonoverlapping receptive fields may be largely independent, whereas they may be strongly interdependent in overlapping receptive fields. It must be noted, however, that "on" responses from non overlapping fields do indeed interact strongly with one another indicating communality of channel. The same may be said for "off" responses.

Two aspects of Phillips and Singer's (1974) explanation were found wanting: bases of judgment and rapid light adaptation. Results from Experiment 1 suggested that the basis of judgment may vary with ISI. Relative magnitudes of neural reponses to the focal and contextual elements may have determined performance at short ISIs in the early portion of the curves in Figures 4 and 5, as Phillips and Singer (1974) proposed, and a more durable memorial representation may have determined performance in the later portion. Phillips and Singer (1974) did not discuss the possibility that different bases of judgment may have determined performance at different ISIs. They did, however, suggest that the basis of judgment may vary with the number of elements in the display.

A discussion of the role of rapid light adaptation was also absent in their explanation. Results from Experiment 3 suggested that rapid light adaptation is an important determinant of performance in the paradigm. In Experiment 3,

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performance was poorer the lower the luminance level of T1. The effect of the luminance level of T1, and the difference between additions and subtractions, both were explained by local changes in adaptation and concomitant changes in sensitivity (see pages 54 and 77).

The results also suggested that the changes in sensitivity were very local, restricted to the immediate area stimulted by the display elements. To date, the local nature of rapid light adaptation has been overlooked. Researchers who have studied rapid light adaptation in the human visual system, most notably Crawford (1947), Boynton (1958), Battersby and Wagman (1959) and White, Kelly and Sturr (1978) have used very large adapting or conditioning fields, typically no smaller than 3° of visual angle. The present research suggests a method for studying local rapid light adaptation. In the present method the adaptation level is determined by the luminance of the elements in T1 and the luminance of the background. Thus the adaptation level of small stimulated and unstimulated areas of retina can be investigated simultaneously.

An experiment testing the limits of the local nature of rapid light adaptation might vary the size and separation of the display elements. Variations in the adaptation level of the inter-element spaces would indicate that the test element was changing the adaptation level of the retinal areas beyond those it was directly stimulating. These variations would be reflected in the detectability of

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additions. In Experiment 2 the difference between additions and subtractions was approximately constant at all levels of density, where performance was below ceiling, suggesting that the adaptation level of the inter-element spaces was constant. If the adaptation level of the inter-element spaces increased as density increased we would have expected performance on additions to deteriorate at a greater rate relative to performance on subtractions. By parametrically varying the size of the display elements and their minimal separation one could discover the conditions where the rate of change in performance on additions changed relative to performance on subtractions, and thus infer the minimal areas of local rapid light adaptation.

One aspect of the present research which was not pursued in detail was the durable memory representation which may have mediated performance at long ISIs in Experiment 1. It may be of interest to extend the ISI between T1 and T2 beyond 320 msec and determine the limits of this memory. It may turn out that it is an iconic representation as defined by Coltheart (1980) who distinguished between two forms of iconic memory: visible persistence and informational persistence. He chose to call the later "iconic memory" and defined it by exclusion. Iconic memory, unlike visible persistence, does not exhibit an inverse relationship between display duration or display luminance and the availability of the memory representation. It is a memory representation that is available for a short

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period after the presentation of a display but is phenomenally invisible. The visible persistence of a display after its offset is nil when the display duration is longer than approx. 100 msec (Di Lollo, 1980). Thus the memory representation which mediated performance at long ISIs in Experiment 1 was not visible and thus cannot be regarded as visible persistence, but may be iconic memory. The representation of the display which mediated performance at short ISIs within the initial portion of the curves in Figures 4 and 5 is neither iconic memory nor visible persistence. The duration of T1 (500 msec) excludes the possibility that it may be visible persistence, and arguments presented on page 29 suggest that it is not a durable form of representation like iconic memory. As discussed earlier (see page 4) it is a short lasting form of inhibition.

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